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OF THE

AUSTRALIAN MUSEUM

VOL. 27

PRINTED BY ORDER OF THE TRUSTEES

SYDNEY, 1966–1969

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The Genus *Chlorinoides* (Crustacea, Brachyura, Majidae). 1. A Redescription of *C. tenuirostris* Haswell and the Status of the Genus *Acanthophrys* A. Milne Edwards

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Figs. 1-11

Manuscript received 20th August, 1964

ABSTRACT

The Indo-West Pacific spider-crab genus *Chlorinoides* is redefined and a key is given to the 12 included species considered to be of good taxonomic standing. The type species, *C. tenuirostris* is shown to be congeneric with several species formerly placed in the genus *Acanthophrys*, which latter genus is now reduced to synonymy with *Hyastenus* White. The genus *Prismatopus* Ward is reduced to synonymy with *Chlorinoides*.

INTRODUCTION

Among the spider crabs of the family Majidae unique to the Indo-West Pacific are the assemblage of species which have been variously referred to the genera *Acanthophrys* and *Chlorinoides*. These small, delicate crabs, with a pyriform carapace set with long spines or flattened plates, or both, and long, slender ambulatory legs, are known from continental shelf depths from Hawaii to South Africa. In the past, while most workers on the group have considered that most of the species belong in a single genus, there has been some difference of opinion on which genus this should be. In this paper the status and relationships of these genera and species are considered.

The genus *Acanthophrys* was set up by A. Milne Edwards in 1865 for two species of majid spider crab, both new to science, *A. cristimanus* from Nuku Hiva in the Marquesas Islands and *A. aculeatus* from the Indian Ocean. Good figures and descriptions of both species were given but no type species was specified. A third species, *A. filholi*, from New Zealand, was later added by the same author (A. Milne Edwards, 1876) and in 1879 a fourth species, *A. paucispina* from the Fiji Islands, was described by Miers (1879a). Shortly afterwards, Miers (1879b) designated *A. cristimanus* as the type species of the genus, which was redefined to include, in addition, only *A. paucispina*.

Haswell (1880) established the genus *Chlorinoides* for a single (new) species from Torres Strait, *C. tenuirostris*, which was considered to be closely related to several species then referred to the genus *Chorinus* Latreille, 1825 by H. Milne Edwards (1834), de Haan (1839) and Adams and White (1848). Following his restriction of the genus *Acanthophrys*, Miers (1884, 1886) transferred to *Chlorinoides* those species of *Chorinus* mentioned by Haswell, together with the remaining species from *Acanthophrys*

and three, formerly referred to *Paramithrax* H. Milne Edwards, 1834, described by himself (Miers 1879a) and by Haswell (1882a, 1882b, 1882c). As thus constituted, *Chlorinoides* was regarded by several subsequent authors including Alcock (1895), as merely a subgenus of *Paramithrax*.

In an important paper some few years after the turn of the century Bouvier (1906) retained the name *Acanthophrys* for the group of species which Miers had included in *Chlorinoides* maintaining that according to a manuscript note left by A. Milne Edwards *A. cristimanus* correctly belonged to the genus *Lahaina* Dana, 1851. Bouvier thus considered *A. aculeatus* A. Milne Edwards to be the type species of *Acanthophrys*. On the other hand Rathbun (1906), in a paper published in the same year, emphasized that any consideration of the possible synonymy of *Acanthophrys* and *Chlorinoides* depended on comparison of *C. tenuirostris* with *A. cristimanus*, not with *A. aculeatus* A. Milne Edwards. Most recent workers, such as Balss (1929), Sakai (1938), Barnard (1950) and Bennett (1964), have followed Bouvier and used the name *Acanthophrys*, while at the same time *A. cristimanus* and *Lahaina ovata* Dana, 1851, have been transferred to the genus *Hyastenus* White, 1847 (see Balss, 1935). The resulting confusion is exemplified by Hale's (1927) short description of the Australian *Paramithrax spatulifer* Haswell as a species of *Chlorinoides*, while the closely related New Zealand species *Acanthophrys filholi* continues to be known under its original generic name (see Dell, 1960); again, while Sakai (1938) and Barnard (1950) describe the widespread *Chorinus longispinus* de Haan, 1839, as a species of *Acanthophrys*, Chhapgar (1957) recently discusses the closely related *Chorinus aculeata* H. Milne Edwards, 1834, under *Chlorinoides* which he regards as a subgenus of *Paramithrax*.

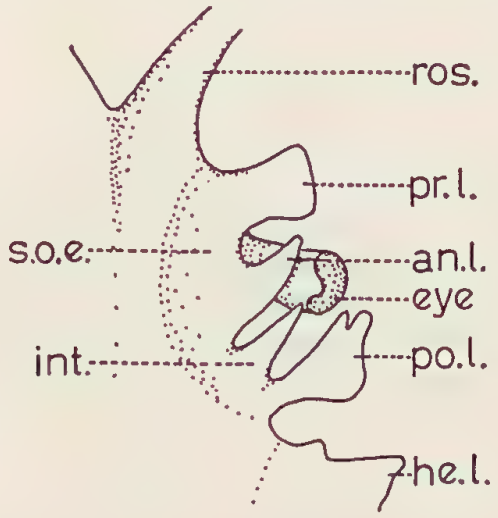


Fig. 1.: Generalized supraorbital detail in the Genus *Chlorinoides*. an.l., antorbital lobe; he.l., hepatic lobe; int., intercalated spine; po.l., postorbital lobe; pr.l., preorbital lobe; ros., rostral spine; s.o.e., supraorbital eave.

Terminology throughout this paper follows that used by Rathbun (1925) and Garth (1958), except for some modifications with respect to the orbit (see fig. 1). Throughout this genus there are four, seldom five, spines or lobes overhanging the orbit. The first two (seldom three) of these, which arise from the supraorbital eave (supraocular eave of some authors), are here named the preorbital (anteriorly) and the antorbital (posteriorly). Behind these and separated from the eave by a deep fissure is the intercalated (intercalary or intermediate) spine. Behind this again, and also separated by a deep fissure, is the postorbital (or postocular) lobe.

The system of measurements follows that used by Garth (1958)

SYSTEMATIC DISCUSSION

Superfamily **OXYRHYNCHA** Latreille, 1803

Family **Majidae** Samouelle, 1819

Subfamily **Majinae** Alcock, 1895; Balss, 1929, restricted

Genus **Chlorinoides** Haswell, 1880

Acanthophrys A. Milne Edwards, 1865: 140 (part: *A. aculeatus* A. Milne Edwards, 1865). Bouvier, 1906: 485. Balss, 1929: 19. Sakai, 1938: 307. Barnard, 1950: 61. Bennett, 1964: 57.

Chlorinoides Haswell, 1880: 442; 1882c: 17. Miers, 1886: 51. Rathbun, 1906: 881.

Paramithrax (*Chlorinoides*) Miers, 1884: 192, 552. Alcock, 1895: 240. Not *Paramithrax* H. Milne Edwards, 1834.

Acantophrys Filhol, 1886: 365 (incorrect subsequent spelling of *Acanthophrys* A. Milne Edwards, 1865).

Prismatopus Ward, 1933: 391; type species, by monotypy: *Prismatopus albanyensis* Ward, 1933.

Description: Carapace subpyriform, inflated, margins and dorsum with a few long spines or lamellate lobes, or both. Rostrum of two long spines, divergent from base. Supraorbital region comprising eave, intercalated spine and postorbital lobe, the three separated by deep fissures; eave with two, usually salient, spines or lamellate lobes; postorbital lobe excavated anteriorly. Eyestalk usually long and slender, almost completely retractile to excavation of postorbital lobe; cornea terminal or subterminal. Basal antennal article leaving orbit incomplete below, longitudinally subrectangular, longer than broad, anterior angles toothed, teeth spiniform or lamellate, lateral tooth directed outwards.

Third maxillipeds with merus as broad as ischium, subquadrate, anterolateral angle not greatly expanded, distal edge notched, a small spine at lateral angle of notch.

Merus, carpus and propodus of cheliped usually with longitudinal ridges or crests. Ambulatory legs slender, longer than carapace, meri usually with one or more distal spines.

Abdomen of seven distinct segments in both sexes.

Range: Indo-west Pacific, including Hawaii, Japan, China, Indonesia, Australia, New Zealand, India, east coast of South Africa.

Type species: Chlorinoides tenuirostris Haswell, 1880, by monotypy; a north-east Australian species. (This species is described below).

List of species: The genus as defined above includes 12 species of good taxonomic standing, as listed below. The approximate relationships of the species are indicated in the form of a key at the end of this paper.

The species are listed here in chronological order of their first description under the specific name by which they are currently known; the original name of the species, of synonymous species and described varieties (if any) are given together with distribution and a reference to the best available description and figure.

Chlorinoides aculeatus (H. Milne Edwards, 1834): *Chorinus aculeata* H. Milne Edwards, 1834; *Paramithrax (Chlorinoides) aculeatus*, var. *armatus* Miers, 1884; Japan, south-east Asia, Indian Ocean, north-east and west Australia; see Miers, 1884: 193, pl. xviii fig. A., and Sakai, 1938: 310, text-fig. 43.

C. longispinus (de Haan, 1839): *Maia (Chorinus) longispinus* (de Haan, 1839); *Paramithrax coppingeri* Haswell, 1882; *Paramithrax (Chlorinoides) longispinus*, var. *bituberculata* Miers, 1884; *Acanthophrys longispinus*, var. *spinossissima* Bouvier, 1906; *Paramithrax (Chlorinoides) longispinus*, var. *bispinosus* Laurie, 1906; Indo-west Pacific from Japan to Mozambique, north-east Australia; see Sakai, 1938: 308, pl. XXI fig. 2.

C. acanthonotus (Adams and White, 1848): *Chorinus acanthonotus* Adams and White, 1848; Borneo; see Adams and White, 1848: 11, pl. I figs. 1, 1a-c.

C. filholi (A. Milne Edwards, 1876): *Acanthophrys filholi* A. Milne Edwards, 1876; New Zealand; see Dell, 1960: 2, figs. 1, 4-6, pl. 1; and Bennett, 1964: 57, figs. 55-57, 124.

C. halimoides (Miers, 1879): *Paramithrax halimoides* Miers, 1879; south-east Asia; see Miers, 1879a: 10; no figure available.

C. tenuirostris Haswell, 1880: north-east Australia; redescribed and figured below.

C. spatulifer (Haswell, 1882): *Acanthophrys aculeatus* A. Milne Edwards, 1865; *Paramithrax spatulifer* Haswell, 1882; *Chlorinoides coppingeri*, Miers, 1886; *Paramithrax (Chlorinoides) coppingeri*, Calman, 1900; not *P. coppingeri* Haswell, 1882; north-east to southern Australia; see Hale, 1927: 137, fig. 138 (as *Chlorinoides spatulifer*).

C. germaini (Bouvier, 1906): *Acanthophrys germaini* Bouvier, 1906; South China Sea; see Bouvier, 1906: 487; no figure available.

C. harmandi (Bouvier, 1906): *Acanthophrys harmandi* Bouvier, 1906; Japan; see Parisi, 1915: 290, pl. 7 fig. 4; or Sakai, 1938: 307, text-fig. 42.

C. goldsboroughi Rathbun, 1906: Hawaii; see Rathbun, 1906: 881, pl. xiv fig. 7.

C. brevispinosa Yokoya, 1933: Japan; see Yokoya, 1933: 159, text-fig. 58.

C. albanyensis (Ward, 1933): *Prismatopus albanyensis* Ward, 1933; north-east Australia; see Ward, 1933: 391, pl. xxiii fig. 3.

Chlorinoides tenuirostris Haswell, 1880

Text-figs. 2-11

Chlorinoides tenuirostris Haswell, 1880: 443, pls. 26 fig. 1; 1882c: 18. Miers, 1886: 51.

Acanthophrys tenuirostris (Haswell), Bouvier, 1906: 486.

Holotype: Male (?). Macleay Museum, University of Sydney. Only doubtfully still extant (Mr. F. A. McNeill, pers. comm.).

Type locality: Darnley Island, Torres Strait.

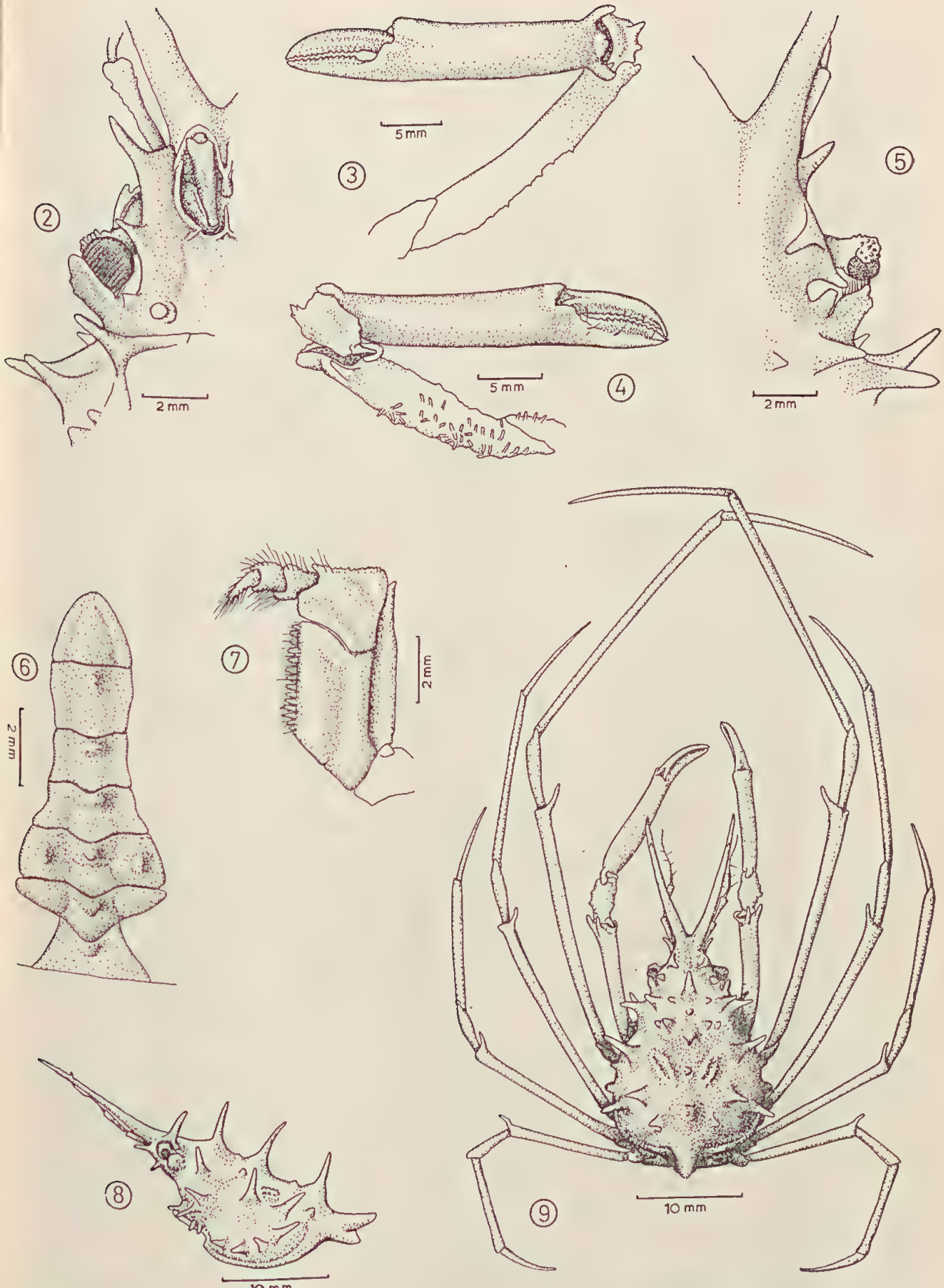
Material examined: Ten specimens as follows:

Macleay Museum, University of Sydney: 1 male, carapace length 22.5 mm, 1 female carapace length 39.5 mm, off Cape Grenville, Cape York Peninsula. [No further data available but Mr. McNeill (pers. comm.) believes the specimens to be over eighty years old.]

Australian Museum, Sydney: 3 males, 5 females, carapace length 18.8-32.8 mm, northern end of Albany Passage, Cape York Peninsula, M. Ward, Aug.-Sept., 1928 (Aust. Mus. No. P. 13941).

Distribution: North-eastern Australia, from Darnley Island to Cape Grenville.

Diagnosis: Rostral spines very long. Preorbital spine directed vertically, simple. A single hepatic spine and a single cardiac spine. Ambulatory legs extremely long, meri with a single distal spine.



Figs. 2-9: *Chlorinoides tenuirostris* Haswell, 22.5 mm male, Cape Grenville (text-fig. 6 only) and 31.7 mm male, Albany Passage. 2, ventral view of orbit; 3, outer view of male cheliped; 4, inner view of male cheliped; 5, dorsal view of orbit; 6, male abdomen; 7, left third maxilliped; 8, lateral view of carapace; 9, dorsal view of whole specimen.

Description: Carapace narrowly pyriform (width slightly less than length), weakly inflated, margins and dorsal surface set with a few long, slender, conical, sharply-pointed spines and short tubercles. All surfaces covered by short simple hairs, closely packed and expanded as " fleshy " lobes, sometimes partly concealing tubercles and spines. Curled hairs in scattered groups on dorsal surface, along posterolateral margin and fringing rostral spines.

Rostrum of two very long (about two-thirds postrostral length of carapace), slender, cylindrical, sharply-pointed spines, separate from close to base and widely divergent, distance between tips almost twice basal width of rostrum, slightly less than half rostral length, a small sharply pointed spine on upper surface about a quarter the length of rostrum from tip.

Hepatic margin with a long, outwardly curved spine, weakly curved backwards distally. Branchial margin with four equidistant tubercles or spines increasing uniformly in length posteriorly, the first a small tubercle, the last a long spine, slightly exceeding hepatic spine, situated subdorsally. Branchial regions bearing more dorsally two additional spines, a posterior one, slightly longer than fourth marginal and opposite third marginal spine and an anterior one, slightly longer again, just forward of second marginal spine; a very small tubercle just in front of this and posteriorly a slightly larger metabranchial tubercle almost opposite fourth marginal spine.

Dorsal surface of carapace with four very long, subequal, subequidistant medial spines, first three slender, sharply pointed, the last stout, somewhat flattened anteroposteriorly, very wide basally, tip rounded: two mesogastric, the first about halfway along that region, the second far back, between hepatic and first marginal branchial spines, a third centrally surmounting tumid cardiac region, fourth almost overlying posterior intestinal margin and directed weakly posteriorly from base. A very small tubercle between mesogastric spines and another, urogastric, behind second mesogastric. Protogastric regions with three small blunt tubercles close to midline and a longer spine lower down, slightly forward of hepatic spine. Several small tubercles in a prominent group at anteromedial corner of branchial regions. Regions of dorsal surface poorly defined.

Orbit consisting above of supraorbital eave, intercalated spine and postorbital lobe, the three separated by wide U-shaped fissures but intercalated spine rather closer to postorbital lobe than to eave; eave narrow, bearing anteriorly a long, acuminate, flattened preorbital spine, directed slightly backward at tip, arising abruptly and vertically from lateral border and a small blunt to sharply pointed, backwardly directed antorbital spine; intercalated spine very short; flattened, subtriangular, broad-based, bluntly pointed; postorbital lobe extending outwards beyond eave, flattened anteroposteriorly, concave anteriorly, margin fringed by long hairs. Eyestalk not very long but reaching postorbital lobe, not concealed in either dorsal or ventral view; cornea subterminal, somewhat ventral, circular, large. Orbit almost circular, incomplete below.

Basal antennal article narrow, but not extremely so, lateral edge straight, medial edge weakly concave, anterolateral angle bearing a long, conical spine directed forwards and slightly outwards, a similar but slightly stouter spine of equal length at posterolateral corner directed outwards and downwards. A large gap between this and base of postorbital lobe only partly occupied by a small suborbital tubercle close to base of lobe. Antennae long, extending almost to tip of rostrum, two subequal basal segments together making up half this length, much stouter than following segments, cylindrical.

Antennular fossae large, longitudinally subovate. Interantennular spine poorly developed, blunt. Anterior process of epistome extremely slender, not quite reaching interantennular spine.

Epistome longer than wide. Mouthfield subrectangular, anterolateral corners produced forwards and outwards as a stout, blunt, slightly flattened spine equal in length to those of basal antennal article. Pterygostomian regions subtriangular, separated by a deep groove from subhepatic regions, bearing close together laterally two short blunt tubercles. Subhepatic regions weakly inflated, a long, conical, bluntly pointed spine arising immediately below hepatic spine, directed downwards, outwards and slightly forwards and visible from above.

Third maxillipeds slightly gaping. Ischium large, subrectangular, longer than broad, medial half of distal edge produced anteriorly, anteromedial corner sharply angled, lateral half straight to bear merus, medial edge very coarsely toothed, overlaid but not concealed by a sparse fringe of long hairs; outer surface excavated medially as a longitudinal groove. Merus subquadrate, slightly wider, but shorter than, ischium, anterolateral edge minutely crenulate, medial edge obtusely crenate, distal edge deeply notched; outer surface excavated as two very shallow longitudinal grooves. Palp arising from notch of, and slightly longer than, merus, cylindrical, the three segments subequal, setose.

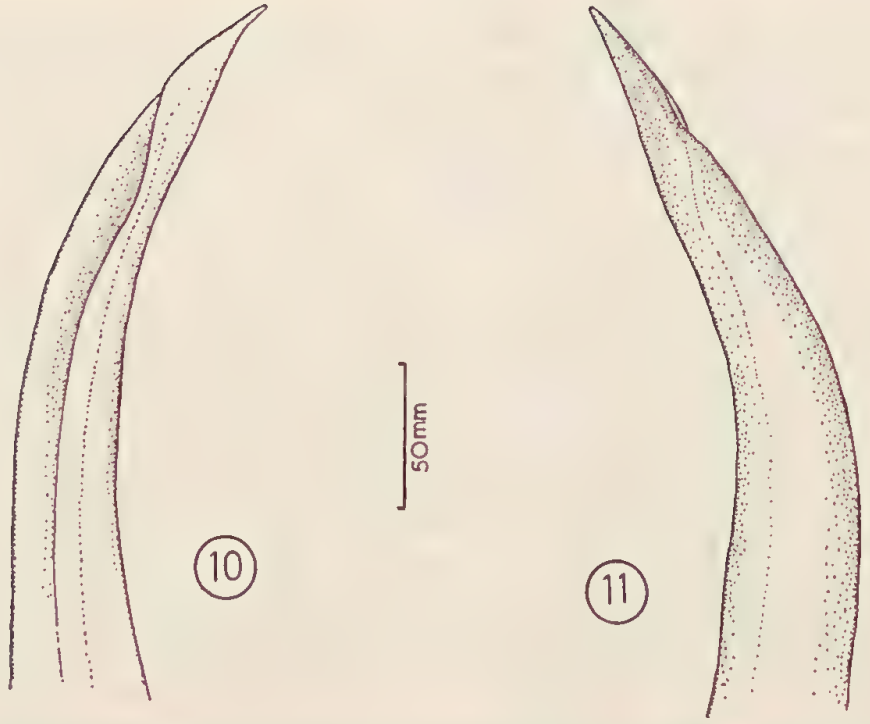
Chelipeds in both sexes of only moderate length, about three-quarters carapace length, very slender, cylindrical except for weakly compressed palm, covered except for most of chela by short simple hairs and scattered longer hairs. Merus long, about two-fifths total length of cheliped, smooth, only a short, curved, sharply pointed spine on dorsal surface distally. Carpus short, smooth except for two small tubercles on dorsal surface, one close to base and one about midway along. Chela long, almost half cheliped, slender, palm weakly expanded distally, dactyl little more than one-third chela; fingers weakly gaping basally, very coarsely toothed along inner edges for distal four-fifths.

Ambulatory legs very long and slender, cylindrical, covered by very short hairs in longitudinal rows, a few scattered long hairs and groups of short, curled hairs on dorsal surface of meri, carpi and propodi; meri bearing distally on dorsal surface a long, weakly curved spine. First leg the longest, almost $2\frac{1}{2}$ times carapace length, following legs descreasing greatly in length, the last only slightly longer than carapace. Meri and propodi very long, subequal, each almost one-third total length of cheliped, dactyli almost half propodi, weakly curved.

Sternum in male extending anteriorly, tapering to a broadly acute spine in midline at posterior border of mouthfield. First three sternites each bearing a small tubercle midway between abdominal fossa and bases of legs, second and third sternites with a second similar tubercle close to outer edge, several smaller tubercles scattered along margin of abdominal fossa; all tubercles hardly discernible, overlain by short hairs.

Abdomen of seven distinct segments in both sexes. Male abdomen narrow, widest at base of third segment, following segments narrowing, abruptly at first, to base of sixth which widens very slightly distally, seventh segment subtriangular, rounded distally. Segments wider than long, subequal in length except for slightly shorter second segment and slightly longer, almost square, sixth segment. Surface elevated in midline as a rounded, longitudinal ridge surmounted distally by a prominent spinous tubercle which decreases in size distally, absent from seventh segment. Third segment with a pair of tubercles laterally, one on each side of midline. Surface of abdomen otherwise smooth. Female abdomen large, covering all of sternum in mature specimen.

Male first pleopod long, stout basally, otherwise very slender, outwardly curved distally, tip very finely pointed, aperture a longitudinal slit on medial surface at end of groove, subterminal; surfaces completely naked except for several stout setae at base laterally and a few very fine setae widely scattered along medial and lateral surfaces for basal third.



Figs. 10, 11: *Chlorinoides tenuirostris* Haswell, 31.7 mm male, Albany Passage, tip of left first pleopod. 10, abdominal aspect; 11, sternal aspect.

Measurements: Largest male: carapace length 31.7 mm, carapace width 15.0 mm, rostral length 14.5 mm, rostral width (basal) 3.3 mm, cheliped 28.5 mm, chelar length 14.5 mm, chelar height 2.5 mm, dactyl 5.4 mm, first ambulatory leg c. 65 mm.

Largest female: carapace length 39.5 mm, cheliped 32.0 mm, chelar length 14.0 mm, chelar height 2.0 mm, first ambulatory leg 84.0 mm.

Remarks: The specimens described here differ little from the type material of *Chlorinoides tenuirostris* according to Haswell's description, although the terminology used in the present paper is slightly different from that used by Haswell. For instance, the large spine on the posterior part of the dorsal surface of the carapace, here called intestinal, is interpreted by Haswell as " cardiac ". The only difference between the present material and that described by Haswell is the presence of a small spinule on the dorsal surface of the rostral spines near the tip, which is not mentioned by Haswell. Reference to Haswell's figures, especially that of the ventral front (Haswell, 1880: pl. xxvi, fig. 1a—" buccal and antennary region "), shows the disposition of the spines and tubercles of the pterygostomian and subhepatic regions to be the same as in the present specimens. Finally, Haswell states that the rostral spines are two-thirds the length of the carapace, by which he presumably means two-thirds postrostral length of carapace. In view of this agreement there can be no doubt as to the specific unity of the specimens described here and the type material of *Chlorinoides tenuirostris* Haswell.

The eight individuals collected by Melbourne Ward in 1928 from Albany Passage are the first well preserved specimens seen since those originally described by Haswell. Although the sample is small numerically some comments can be made on the biology of the species. Most remarkable are the " fleshy " lobes which cover the carapace, including the outer maxillipeds and abdomen. These appear to be simple hairs expanded in some way by intake of water. If the carapace is allowed to dry, these hairs exactly resemble the simple hairs possessed by most other spider crabs. The extremely strong teeth of the chelar fingers and of the outer maxillipeds surely point to this species being a macrophagous feeder.

This species does not appear to mature below a total carapace length of about 25 mm, females smaller than this not having the abdomen fully expanded. There is very little difference in the relative size of the chela in males and females, an unusual feature in this family; the small size of the chela is also uncommon.

The ratio rostral length/carapace length varies from 0.34 to 0.46, all males having a value above 0.40, while only one female has a value greater than this. It must be remembered, though, that the sample is very small, so that such differences may not be consistent.

In the smallest specimen, a male, carapace length 18.8 mm, the intercalated spine appears relatively smaller than in larger specimens, but a much larger series would be needed to show whether this spine does increase in relative size during growth.

This species differs from other species here included in the genus *Chlorinoides* in several features, the most important being the narrow basal antennal article and the shape of the male abdomen. In addition there is almost a complete lack of the flattened " lamellate " or " spatuliform " plates so characteristic of many species of the genus. However, this last character cannot be taken as diagnostic of the genus, and the form of the supraorbital margin with a preorbital, antorbital, intercalated and postorbital lobe, the double rostrum, seven-segmented abdomen, distally spined ambulatory meri, anteriorly toothed basal antennal article, and subquadrate, distally notched merus of the third maxilliped hardly leaves room for disagreement with those previous workers who considered this species to be congeneric with H. Milne Edwards's *Chorinus aculeata*, A. Milne Edwards's *Acanthophrys aculeatus*, de Haan's *Chorinus longispinus* and those other species which over the years have become grouped together within A. Milne Edwards's *Acanthophrys* or Haswell's *Chlorinoides*. Among this group of species *Chlorinoides tenuirostris* undoubtedly stands closest to *C. acanthonotus* (Adams and White, 1848) in the possession of a vertically directed preorbital spine and single long hepatic spine. From the latter species, *C. tenuirostris* is easily distinguished by the simple form of the preorbital spine and the possession of but a single cardiac spine.

Naxiodes robillardi Miers, 1882, at present placed in the subfamily Pisinae, resembles *C. tenuirostris* in the general form of the orit, shape of the basal antennal article, shape of the male abdomen, in the possession of very long rostral spines and of spines on the distal edge of the dorsal surface of the meri of the legs. However, *N. robillardi* grows to a very much greater size than any species here placed in *Chlorinoides* and differs from them also in having many more, somewhat shorter, spines on the carapace.

GENERAL DISCUSSION

The first point to consider is the systematic position of A. Milne Edwards's *Acanthophrys cristimanus*, on which rests the status of the genus *Acanthophrys* A. Milne Edwards, 1865, since that species was validly designated type species of the genus by Miers (1879b). The relationships of *Lahaina ovata* Dana, 1851, type species (by monotypy) of the genus *Lahaina* Dana, 1851, are also important since *A. cristimanus* was stated by Bouvier (1906) to belong to *Lahaina* (*fide* A. Milne Edwards's manuscript note). Comparison of these two species, *A. cristimanus* and *L. ovata* (from the descriptions and figures of A. Milne Edwards, 1865, in the case of the former, and those of Dana, 1852, in the case of the latter), reveals certain important similarities. The two species agree in the form of the upper orbital border (lacking an intercalated spine, consisting only of an unarmed supraorbital eave and a postorbital lobe), of the basal antennal article (narrow, with the anterolateral tooth spinous and forwardly

directed), and of the third maxillipeds (merus laterally expanded and distally unnotched). This agreement is certainly of sufficient importance to warrant the two being considered congeneric. These characters are typical, not of species so far included in *Acanthophrys*, but of species belonging to the genus *Hyastenus* White, 1847. Thus, they should, together with *Acanthophrys paucispina* Miers, 1879, be transferred to the latter genus. [*L. ovata* was first transferred to *Hyastenus* (subgenus *Chorilia*) by Miers (1884: 522)]. *Acanthophrys* is therefore a synonym of *Hyastenus* and unavailable for the group of species which Bouvier (1906), Balss (1929), Sakai (1938) and others have united under that name. Further, Bouvier's grounds for using the name, viz., by rejecting *A. cristimanus* as type species of the genus in favour of *A. aculeatus* A. Milne Edwards, must be regarded as quite invalid. Since *Chlorinoides tenuirostris* Haswell, 1880, has been shown to be congeneric with those species formerly placed in *Acanthophrys*, the name *Chlorinoides* Haswell, 1880, is available and must be used. The separation of *C. tenuirostris* in a distinct genus (by Haswell, 1880: 442) solely on the characters of the greater length of the rostral spines and ambulatory legs has been upheld neither in the past nor by the present study.

The inclusion within this group of species, by Balss (1929), of the Indian Ocean species *Entomonyx spinosus* Miers, 1884 (=*Macrocoeloma nummifer* Alcock, 1895), must now be considered. Balss stated that this species does not belong to the genus *Macrocoeloma* Miers, 1879, because of its possession of an intercalated spine above the orbit. Although the importance of the presence or absence of an intercalated spine has not received as much emphasis in recent years (see Sakai, 1938: 203; Garth 1958: 8) as Balss originally accorded it, it is still very important at the generic level. Therefore Balss's reason for excluding *E. spinosus* from *Macrocoeloma* seems justified. However, the nature of the orbit in this species surely excludes it from *Chlorinoides* for, as may be seen from Miers's original description and figures (Miers, 1884: 526, pl. 47 fig. B,), the supraorbital eave and basal antennal article are laterally expanded, the orbit thereby becoming almost tubular, the carapace thus losing the pyriform shape so typical of species of *Chlorinoides* while the rostral spines are shorter than usually found in the latter genus. Sakai (1938: 309, pl. xxxi, fig. 3) followed Balss in the inclusion of this species in *Acanthophrys*. Although it is clear from his description that the disposition of the spines on the carapace is the same as found in species of *Chlorinoides*, that the ambulatory meri possess a terminal spine and that the spines of the carapace possess terminal knobs, the first two of these do not outweigh the differences in orbital details, while as far as the third is concerned it should be noted that knobbed spines are found in species of other genera, notably several belonging to the genus *Micippa* Leach [see Sakai, 1938: 312, e.g. *M. philyra* (Herbst)]. In orbital characters, *E. spinosus* resembles those species at present placed in the subfamily Mithracinae Balss (see Garth, 1958: 346) and not the Majinae, in which *Chlorinoides* belongs. Consequently, the genus *Entomonyx* Miers, 1844, should be resurrected to contain this single species, *Entomonyx spinosus* Miers, 1884.

The genus *Prismatopus* was set up more than 30 years ago by Melbourne Ward (1933) to contain a (new) species of majid crab, *P. albanyensis* from Albany Passage, north Queensland. Ward related his genus to *Acanthophrys* A. Milne Edwards as defined by Miers (1879b) and gave four points which distinguished *Prismatopus*. In two of these, the laterally directed spine of the basal antennal article, and the notched merus of the third maxillipeds, Ward's species clearly does not belong in *Acanthophrys* A. Milne Edwards as defined by Miers, but in *Chlorinoides* as here defined. The remaining two characters, the trigonal (" triprismatic ") ambulatory legs and the carinate margins of the maxillipeds, are not sufficient to separate this species generically from *Chlorinoides tenuirostris*. Further examination of Ward's description does not produce additional reasons for the retention of a distinct genus. Therefore *Prismatopus* Ward, 1933, is here reduced to synonymy with *Chlorinoides* Haswell.

It seems worthwhile to review now the status of the twelve species included here in *Chlorinoides*. In several cases, forms originally considered distinct species have been later regarded as only varieties of previously described species; in others, specimens differing in a few features have been described as varieties. As Professor Ernst Mayr, in *Animal Species and Evolution* (Harvard University Press, 1963) has recently pointed out, the variety, anything that deviated from the ideal type of the species, was the only subdivision of the species recognized by early taxonomists. The term has no standing under the present zoological nomenclature. It must be decided whether or not any of these varieties should be considered distinct species; so little material is available that the time is not ripe for a consideration of the existence of subspecies. Miers (1884: 182, 193, pl. xviii, fig. A.) described a variety of *C. aculeatus* (H. Milne Edwards, 1834), which he called *Paramithrax* (*Chlorinoides*) *aculeatus*, var. *armatus*. The specimens from Queensland, on which this variety was based, differed from the typical form of *C. aculeatus* only in the shape of the postorbital lobe, which was slightly more expanded distally and partially subdivided into two. Miers himself remarked that such a difference is hardly sufficient to warrant specific separation. Four varieties of *C. longispinus* (de Haan) have been described. The first, originally described as a species of *Paramithrax*, *P. coppingeri*, by Haswell (1882b: 750) was first regarded as a variety of *C. longispinus* by Bouvier (1906). It differs from the typical *C. longispinus*, as understood in Haswell's time, in having none of the supraorbital spines recurved, and two, instead of one, intestinal spine. However, Sakai (1938: 308) describes Japanese specimens of *C. longispinus* as possessing two intestinal spines, Grant and McCulloch (1906) point out that the type specimen of *P. coppingeri* does, in fact, have the antorbital spine recurved, while this, and other species of the genus show some variation as to the degree of curvature of the supraorbital spines (Griffin, unpublished). Therefore, Haswell's species is probably a synonym of *C. longispinus*. Miers (1884: 522) described a variety of *C. longispinus* which he called *P.* (*C.*) *longispinus* var. *bituberculata*, from Darros and Providence Islands, which was distinguished from the typical *C. longispinus* by the possession of a tubercle on the fixed finger and dactyl of the chela. Such a difference can almost certainly be regarded as falling within the normal variation of *C. longispinus*. *Acanthophrys longispinus*, var. *spinossissima*, described by Bouvier (1906: 487, 489) from specimens taken near Mozambique, differs from the typical *C. longispinus* in the absence of a preorbital spine and the presence of two distal spines on the ambulatory meri, while the spines of the carapace are longer than in the typical form and the rostrum is depressed towards the base. Of these four differences only the first two warrant consideration. The absence of the preorbital spine at the moment seems important and unique but the presence of a second distal spine on the ambulatory meri was noticed in a single specimen of *C. longispinus* from Queensland by Grant and McCulloch (1906). At present then, Bouvier's variety is not considered to warrant independent specific status. Laurie (1906) described *Paramithrax* (*Chlorinoides*) *longispinus* var. *bispinosus* from off Ceylon, which differed from de Haan's species "in the absence of the most anterior of the three supra-ocular spines" (Laurie 1906: 383). This variety appears to be the same as Bouvier's var. *spinossissima* and the remarks just made about the latter apply to Laurie's variety also.

In the past several authors (Alcock, 1895; Bouvier, 1906; Sakai, 1938; Barnard, 1950) have regarded the terminal knobs, so often found on the spines of *C. longispinus*, as being diagnostic of this species. It must be emphasized therefore that these knobs are not present in all specimens of this species (Miers, 1884: 192; Grant and McCulloch, 1906; Yaldwyn, pers. comm.), but are present in some specimens of *C. aculeatus* (H. Milne Edwards) (see Sakai, 1938: 310).

Bouvier (1906: 489) and Grant and McCulloch (1906) independently showed that *Acanthophrys aculeatus* A. Milne Edwards, 1865 (not *Chorinus aculeata* H. Milne Edwards, 1834) was conspecific with *Paramithrax spatulifer* Haswell (see Haswell, 1882a: 540). With the inclusion of *Chorinus aculeata* H. Milne Edwards, in the same

genus, *Acanthophrys aculeatus* A. Milne Edwards becomes a junior homonym of *Chorinus aculeata* H. Milne Edwards and therefore requires a new specific name. As Haswell's *spatulifer* is available it must be used. As pointed out by several authors (Grant and McCulloch, 1906; Bouvier, 1906; and Barnard, 1950), Miers (1886) misidentified *C. spatulifer* and described and figured it under the name *Chlorinoides coppingeri*, thus causing some confusion in locality records, notably by Calman (1900). *C. spatulifer* is mainly southern in distribution, being known mostly from south and south-east Australia, while *C. longispinus* (syn. *C. coppingeri*) is a subtropical and tropical species.

Finally, some comments on the distinctness and relationships of *Chlorinoides* itself are fitting. As noted already, *Chlorinoides* was regarded as a subgenus of *Paramithrax* H. Milne Edwards, 1834, by Miers (1884), Alcock (1895) and several other authors. *Chlorinoides* differs from *Notomithrax* Griffin (formerly *Paramithrax* H. Milne Edwards, in part—see Griffin, 1963) and *Leptomithrax* Miers, the taxonomic descendants of *Paramithrax* as originally set up, in several very noticeable features. First (in *Chlorinoides*) the rostral spines are longer, more slender and more divergent; secondly, there is a strong preorbital lobe; thirdly, the postorbital lobe is excavate and generally lamellate; fourthly, the anterolateral tooth of the gasal antennal article is directed strongly outwards rathern than forwards; fifthly, the carapace is smooth rather than densely spinous or tuberculate; and lastly, the ambulatory meri possess a strong distal spine. Nevertheless, some species of *Leptomithrax* and species of *Chlorinoides* do resemble each other in the form of the postorbital lobe and of the basal antennal article. While several species of *Leptomithrax* possess a preorbital lobe, this structure never reaches the state of development seen in species of *Chlorinoides*, and the postorbital lobe is never lamellate. In general, then, species of *Chlorinoides* may be distinguished from those of *Leptomithrax* by the presence of lamellate lobes on, and by the generally smooth appearance of, the carapace. Examples of species of *Leptomithrax* which approach a *Chlorinoides* facies include the Japanese *L. bifidus* (Ortmann) in which the rostral spines are long, slender and outwardly curved distally, the Australian and New Zealand *L. tuberculatus* (Whitelegge) in which the carapace is smoother than in most other species of the genus, and the New Zealand *L. richardsoni* Dell which possesses a strong preorbital spine. It remains only to say that knowledge so far lacking, in most cases, of the shape of the male abdomen and first pleopod should help substantially in working out precise relationships of species of this and related genera.

A key to the 12 species of *Chlorinoides* recognized here can now be given.

KEY TO THE SPECIES OF THE GENUS CHLORINOIDES HASWELL

1. Preorbital and antorbital lobes spinous, not markedly expanded as lamellate lobes 2
   Preorbital or antorbital lobe, or both, a wide, flattened lamella 9

2 (1) Preorbital spine more than 3 times antorbital in length, vertically directed upward from base. Hepatic margin with a single long spine extending laterally beyond postorbital lobe..... 3
   Preorbital spine never more than 1½ times antorbital in length, outwardly directed at least basally. Hepatic margin with a small bilobate lamella 4

3 (2) Preorbital spine bifid at tip. Branchial margin with two long spines posteriorly. Cardiac spine bifid for about distal half. Posterior intestinal margin with two medial spines, the anterior directed upward, posterior directed backward..... *C. acanthonotus* (Adams and White)
   Preorbital spine simple, acuminate. Branchial margin with one long spine posteriorly, two long spines on branchial regions dorsally. A single acuminate cardiac spine. A single flattened, blunt intestinal spine..... *C. tenuirostris* (Haswell)

4 (2) Branchial margin with a small lamella anteriorly followed by three spines. Intestinal region smooth or with a low spine, cardiac region surmounted by a pair of low, submedial spines 5

Branchial margin lacking a small lamella anteriorly, one or two long spines posteriorly. Intestinal and cardiac regions with long spines.. 6

5 (4) Mesogastric region with a single spine posteriorly. Preorbital lobe an acute spine, antorbital lobe rounded distally.. *C. brevispinosa* Yokoya

Mesogastric region with two medial spines. Pretorbital and antorbital lobes subtruncate distally..... *C. goldsboroughi* Rathbun

6 (4) Two long branchial spines posteriorly. Rostral spines outwardly curved, widely divergent, distance between tips about twice rostral length 7

A single long branchial spine posteriorly. Rostral spines weakly divergent, distance between tips not more than two-thirds rostral length 8

7 (6) A single preorbital spine. A single cardiac spine. Intestinal region with two medial spines..... *C. aculeatus* (H. Milne Edwards)

Two preorbital spines distinct from base. A pair of widely divergent submedial cardiac spines. Intestinal region with a single spine .... *C. longispinus* (de Haan)

8 (6) Cardiac region with a single spine. Postorbital lobe a wide lamella.. ..... *C. halimoides* (Miers)

Cardiac region with a pair of submedial spines. Postorbital lobe narrowly subtriangular..... *C. harmandi* (Bouvier)

9 (1) Posterior intestinal margin with a prominent lamellate lobe. Ambulatory legs cylindrical 10

Posterior intestinal margin with an acuminate spine. Ambulatory legs trigonal..... *C. albanyensis* (Ward)

10 (9) Branchial margin with a single spine posteriorly. Cardiac region with a single acuminate spine. Preorbital and antorbital lobes fused basally as a wide lamella, distinct as two short spines distally .... *C. germaini* (Bouvier)

Branchial margin with two long flattened spines posteriorly. Cardiac region surmounted by a flattened lobe, bifid for distal half. Preorbital and antorbital lobes distinct from base 11

11 (10) Preorbital lobe lamellate, wide, summit truncate or concave, antorbital lobe a short spine. Medial margins of rostrum armed with several short spines. Posterior intestinal lobe widest midway from base, summit rounded..... *C. spatulifer* (Haswell)

Preorbital lobe slender, spinous, acuminate, antorbital lobe lamellate, distally expanded and anteriorly directed. Medial margins of rostrum lacking spines. Posterior intestinal lobe widest at base, summit truncate to concave..... *C. filholi* (A. Milne Edwards)

SUMMARY

1. The status of the genus *Acanthophrys* A. Milne Edwards, 1876, based by the subsequent designation of Miers in 1879 on *A. cristimanus* A. M. Edw., 1865, is briefly reviewed. *A. cristimanus* is shown to belong to *Hyastenus* White, 1847, and is transferred, together with *Lahaina ovata* Dana, 1851, type species of *Lahaina* Dana, 1851, and *Acanthophrys paucispina* Miers, 1879, to that genus. *Acanthophrys* and *Lahaina* are therefore synonyms of *Hyastenus*.

2. The genus *Chlorinoides* Haswell, 1880, based on *C. tenuirostris* Haswell, 1880, is redefined and shown to be a distinct genus most closely related to *Leptomithrax* Miers, 1876. Comparison of those species formerly included in *Acanthophrys* with *C. tenuirostris* shows that the vast majority are congeneric with that species.

3. The monotypic genus *Prismatopus* Ward, 1933, is reduced to synonymy with *Chlorinoides*.

4. The monotypic genus *Entomonyx* Miers, 1884, is resurrected for *E. spinosus* Miers, 1884. This species was first included in *Acanthophrys* by Balss in 1929 but does not belong in *Chlorinoides* as here constituted.

5. Twelve species are included in *Chlorinoides*. Their status and relationships are discussed. None of the varieties so far described are considered to be distinct species. A key to the 12 species is given.

6. *Chlorinoides tenuirostris* is redescribed in detail and figured on the basis of new material. Some brief notes are given on its biology and relationships.

ACKNOWLEDGMENTS

This work was initiated during studies for the degree of M.Sc. at Victoria University of Wellington, New Zealand, and I would therefore like to thank Professor L. R. Richardson, recently retired from the Department of Zoology of that University, for his helpful advice. The continuation of these studies, and particularly the review of species, was made possible by Dr. J. W. Evans, Director, and the Trustees, of the Australian Museum, Sydney, kindly making available facilities at that Museum during May and August, 1962, and again during January, 1963. I wish to thank Mr. F. A. McNeill, of the Museum, for his kindness in obtaining for me specimens of *C. tenuirostris* from the Macleay Museum. For helpful discussion of some of the problems dealt with here I wish to thank Professor H. B. Fell, Dr. P. M. Ralph and Dr. D. L. Pawson, all of the Victoria University of Wellington Zoology Department, and Dr. J. L. Hickman, University of Tasmania Zoology Department. Finally, I would like to thank very sincerely Dr. John Yaldwyn, Australian Museum, for sending me material in his care and for his constant encouragement and helpful advice throughout the preparation of this paper.

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STUDIES ON POLYZOA (BRYOZOA) FROM THE *ENDEAVOUR* EXPEDITION, 1909-1914

I. A NEW LUNULITIFORM POLYZOAN (ASCOPHORA) FROM SOUTH-EAST AUSTRALIA

II. COLONY FORMATION IN *SELENARIA NITIDA* MAPLESTONE

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Plates 1 and 2. Figure 1

Manuscript received 2nd December, 1964

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I. A New Lunulitiform Polyzoan (Ascophora) from South-east Australia

ABSTRACT

A monotypic family is erected in order to accommodate a new lunulitiform ascophoran polyzoan, referred here to *Australiana* n.gen. Family characteristics comprise the cupuliform zoarium with quadrate zooecia radially arranged in single or double rows. The dimorphic orifice is elongate in ordinary zooecia and transversely elliptical in fertile zooecia. A pair of large fenestrae perforate the outer wall of the ectooecium. The basal surface, strongly concave in mature zooecia, is perforated by large foramina, interpreted as kenozooecia, and bears several radicular chambers. Avicularia are not developed. The species is known as a fossil from the lower Muddy Creek (Middle Miocene) beds of Victoria, and from the Recent Peronian faunal province.

INTRODUCTION

The characters of the genus here described, including the remarkably regular arrangement of the zooecia not covered by a mass of secondarily formed avicularia and convexities, as well as the distinctive fenestrate ovicells, clearly distinguish it from other previously described lunulitiform ascophoran genera, and therefore justify its reference (as the type genus) to a new family.

AUSTRALIANIDAE new family

Diagnosis: As for the genus.

Australiana new genus

Type species (here chosen): *Australiana bifenestrata* n.sp. (see below).

Diagnosis: Loosely attached, cupuliform, unilaminar Ascophora with a thin porcellanous frontal wall. Zooecia quadrate, radially arranged in uniserial or biserial rows, extending vertically from the frontal to the basal surface. Orifice dimorphic, the proximal end directed towards the apex of the zoarium, elongate in ordinary zooecia, with two condyles at the proximal third; transversely elliptical in fertile zooecia. Ovicell entozooecial, with a pair of conspicuous frontal pores perforating the outer wall of the ectooecium. Ancestrula membraniporine, apical, giving rise to three first-generation zooecia. Basal surface deeply concave in mature zooecia, with large foramina and scattered radicular chambers. Avicularia wanting.

Remarks: The holotype (plate 1, fig. 5) is chosen from material retrieved by the *Thetis* Expedition (1898) off Bulgo, New South Wales. Additional paratypic material was taken near Gabo Island, Victoria; Bass Strait; and off the New South Wales coast by the *Endeavour* Expedition (1909-14). I have also examined three specimens collected off New South Wales by members of the Australian Museum, also a single specimen from Port Jackson, N.S.W.

The majority of this material was examined some time before 1921 by R. Bretnall, of the Australian Museum staff. He identified this form as a new species of the genus *Lunularia* but his manuscript name was never published, nor is it mentioned in the unpublished and incomplete Bretnall manuscript on the Polyzoa of the *Endeavour* Expedition.

Ecology: Like other lunulitiform as well as some eschariform species, *Australiana bifenestrata* n.sp. favours a " small particle " substrate (Lagaaij 1963: 187). The sea bottom off Gabo Island, Victoria, appears to be an especially suitable environment to judge from the abundant zoaria of *Lunulites*, *Selenaria*, *Conescharellina* as well as the loosely attached eschariform *Lanceopora obliqua* (MacGillivray) and *L. macneilli* (Livingstone), in the *Endeavour* collections of Polyzoa from this area.

It should be noted, however, that the present species is not restricted solely to a firm biotope. The substrate of the type locality (off Bulgo, N.S.W.), for example comprises " mud and abbatoir refuse " (Waite 1899: 22). This tolerance for a soft biotope is doubtless due to the fact that *A. bifenestrata* lives " loosely attached ", anchorage being provided by its chitinous radicles, hence the actual consistency of the substrate is not of the critical importance it is for the encrusting polyzoa.

Australiana bifenestrata* n.sp.

(Text-fig. 1, a-i; plate 1, figs. 1-7)

*with reference to the bifenestrate ovicells

1895 "*? Lunulites angulopora* Tenison-Woods," MacGillivray, p. 46, pl. 8, fig. 1, (not *L. angulopora* Tenison-Woods, 1880, p. 7, pl. 1, fig. 3a-c = *Conescharellina angulopora*).

Holotype: Australian Museum Cat. No. U. 4022; locality, off Bulgo, New South Wales, south-by-east, 6-8½ miles from shore, 59-63 fathoms. *Thetis* Expedition, Station 47, 16.3.1898.

Diagnosis: As for the genus.

Description: Zoarium dome-shaped, loosely attached, attaining a maximum diameter of 5.0 mm and a height of 2.3 mm.

Explanation of Text-Figure 1, a-i, (opposite)

Australiana bifenestrata n.gen. n.sp.

Fig. a: Four ordinary zooecia and a fertile zooecium, with a bifenestrate ovicell.

Fig. b: Longitudinal section through a fertile zooecium, showing the oval brood chamber. A kenozooid lies below, communicating with adjacent zooecia by means of basal septula.

Fig. c: Two distal walls with basal septula, one wall swollen by the impingement of the internal ovicell.

Fig. d: Lateral wall; note the multiporous rosette plate.

Fig. e: Ordinary operculum with occlusor muscles attached.

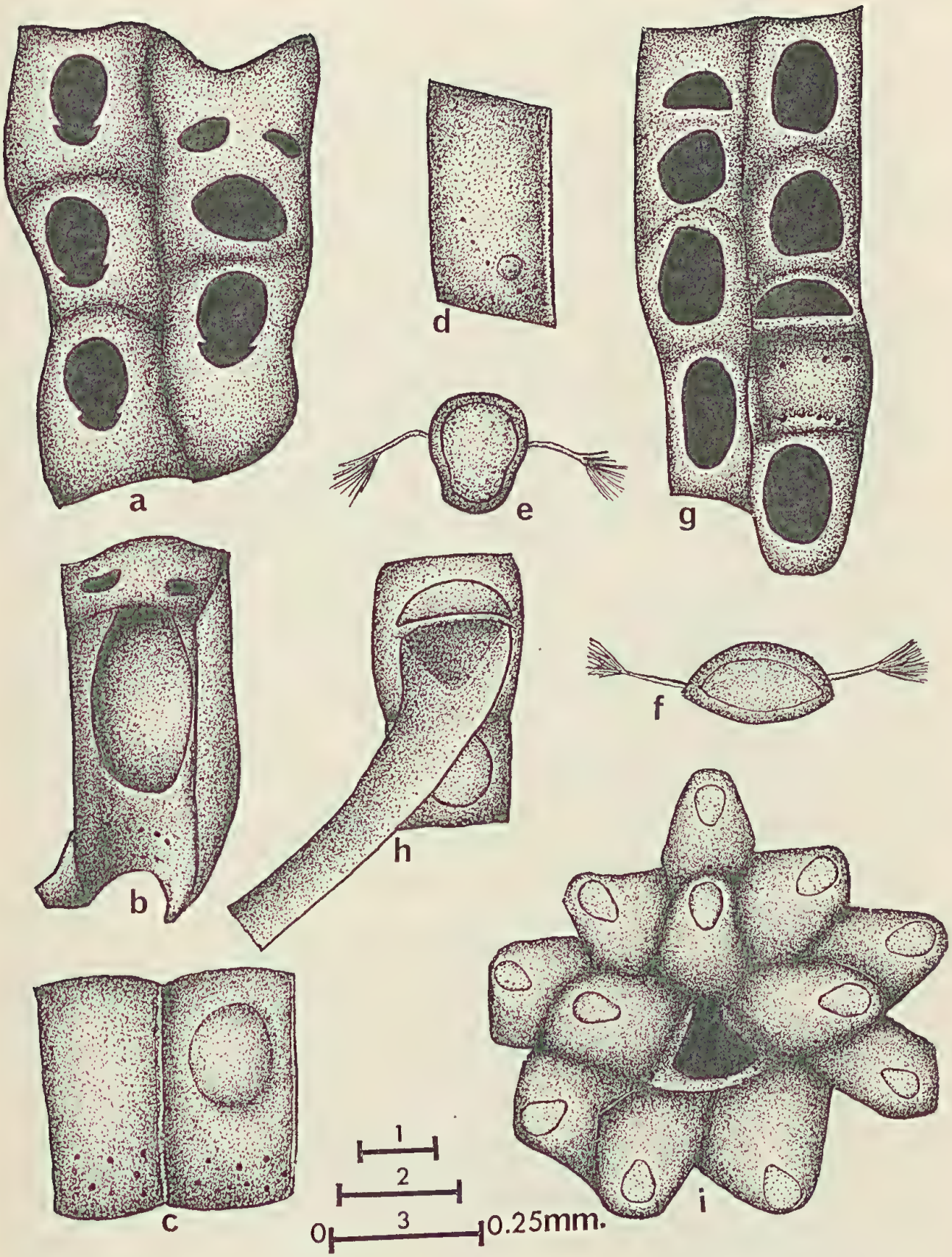
Fig. f: Fertile operculum.

Fig. g: Basal surface to show the foramina. The following explanation reads from the distal to proximal margins. Left row—foramen of kenozooid below the ovicell, followed by foramen of fertile zooecium; then two foramina of ordinary zooecia. Right row—two foramina of ordinary zooecia; foramen of radicular chamber, then a foramen of an ordinary zooecium.

Fig. h: Root chamber with radicle.

Fig. i: Apical view of colony to show the arrangement of early formed zooecia. Note the 3-5 sequence of periancestrula zooecia comprising the 1st and 2nd generations respectively. The proximal four zooecia form part of the third-generation.

Figs. a, b, c, d, g are drawn from calcined material. Figs. a, b, c, d, g, h are drawn to scale 2. Figs. e and f drawn to scale 3. Fig. i drawn to scale 1. All figures are from *Endeavour* material taken off Gabo Island, Victoria.



Text-fig. 1, a-i.

Zooecia quadrate, reaching the basal surface of the colony, radially arranged in uni- or biserial rows, forming regular circlets extending in a vertical direction from the apical ancestrula. Interzooecial furrows broad, not distinct. *Orifice* dimorphic, elongate in ordinary zooecia, anter rounded distally, sides converging posteriorly, constricted at the proximal third by two minute condyles, widening into a shallow poster proximally; transversely elliptical in fertile zooecia, condyles not developed. *Opercula* chitinous, finely pitted, and with a complete marginal sclerite, projecting at each margin as two triangular flanges attached by a pair of long occlusor muscles to the lateral walls. Two divaricator muscles originate from each lateral wall passing obliquely towards the frontal surface and inserting into the basal sclerite of the operculum. *Peristome* slightly raised as a salient rim around the distal margin of the orifice, oral spines wanting. *Frontal surface* thin, porcellanous, convex, reduced, traversed at irregular intervals by concentric growth laminae, often bearing scattered pustules. *Ovicells* entozooecial, usually occurring close to the margins of the colony. Outer wall of the ectooecium perforated by two prominent fenestrae covered by chitinous membranes. Inner wall slightly calcified, immersed in the distal region of the zooecial cavity, impinging upon the distal wall to form an oval brood chamber, extending two-thirds the length of the zoarium, delineating a small chamber beneath. *Basal surface* deeply concave, particularly in adult zoaria, with prominent circular or longitudinally elliptical foramina, each foramen covered by a chitinous membrane and surrounded by a low ridge. *Radicular chambers* scattered among the basal foramina, enlarged, quadrate, with a horizontal plate perforated by several small septula, and a semi-elliptical foramen distally; giving rise to long strap-like radicles or capsular chambers. *Zooecial walls* long and narrow, each provided with a zig-zag row of 8-10 septula, or one or two rosette plates within the basal margin. *Ancestrula* membraniporine, frontal wall incomplete, the operculum not completely differentiated from the frontal membrane; generating three zooecia distally. *Avicularia* not developed.

Measurements: The measurements used, and the terminology employed here, are defined in Brown (1952: 33-34).

	Lz = 0.30 — 0.38 mm.	lz = 0.25 — 0.30 mm.
	hr = 0.15 — 0.17 mm.	lr = 0.10 — 0.12 mm.
Ovicelled zooecia	hr = 0.10 mm.	lr = 0.17 mm.

Distribution: (a) Fossil: Muddy Creek (lower beds), (Balcombian, Middle Miocene). National Museum Collection, Victoria.

(b) Recent: Off Gabo Island, Victoria; Bass Strait; Port Jackson, N.S.W.; off the coast of New South Wales.

Other material examined: (All material listed below has paratype status. All catalogue numbers are from the Australian Museum collections).

I. South of Gabo Island, Victoria. 100-200 fathoms. E.6341, E.6342, E.6427, E.6483. Additional material from this locality has been sorted from bulk polyzoan collections, retrieved by the Commonwealth Fisheries Investigation ship *Endeavour* 12.9.1914 (spirit preserved material U. 4021).

II. 20 miles East of King Island, Bass Strait. E.6362. Collected by C.F.I.S. *Endeavour* 21.6.1909.

III. *Thetis* Expedition, Station 47. Off Bulgo, N.S.W. U:1311.

IV. E.6802. Off Twofold Bay, N.S.W. 30-50 fathoms. C.F.I.S. *Endeavour* 30.9.1914.

V. 2½-4 miles off Botany, N.S.W. 33-56 fathoms. U.985, U.997.

VI. Port Jackson, N.S.W. U.1004. (Comprises a single fragmented specimen, presented by Dr. Porter).

VII. U.1282. *Thetis* Expedition, station not known.

Remarks: The orientation of the polypide (desiccated, owing to the dry preservation of the material) in the tubular exoskeleton of this species conforms with Harmer's (1957: text-fig. 68B) interpretation of polypide orientation within the conescharellinid zooecium. In many instances the thin membranous compensatrix is still retained, forming a large spacious sac that extends almost the full length of the zooecium. Vestiges of the powerful retractor muscles are attached near the base of the proximal walls.

Though the function of the basal foramina is not known, they would appear to be comparable to the cancelli of some Conescharellinidae. The foramina in the present species, however, are not aviculiferous; they have a variety of shapes (text-fig. 1, g), ranging from circular in wide zooecia to elliptical in narrower individuals. Canu and Bassler (1928: 153, 154) interpreted comparable structures in *Mamillopora* as " hydrostatic chambers " in accordance with their hypothesis of a pelagic habitat for that genus. As with the conescharellinid cancelli, I interpret these structures as heterozooecia, or more precisely, kenozooecia, in so far as they lack a polypide or musculature. The chamber beneath the ovicell would also seem to qualify as a kenozooecium, communication with adjacent zooecia being provided by basal septula.

Interspersed among the basal foramina are specialized radicular chambers (approximately eight occurring in a mature colony), which give rise to the long strap-like radicles (text-fig. 1, h). The radicular chambers are recognized by their quadrate outline (plate 1, fig. 6), and considerably larger size compared to the foramina. A salient ridge separates the perforated radicular plate from the transversely semi-elliptical foramen distally. This foramen appears to be comparable to the crescentic slit of the lunoecium in the Conescharellinidae. Unlike lunoecia, however, the present chambers are restricted to the basal area. Their long radicles are inserted into the radicular plate (text-fig. 1, h) and intertwine as an anchoring filament attached to foraminifera or fragmentary polyzoan colonies. The large globular capsules observed on some chambers are probably developing tubes similar to those Silén (1947: 37, 46) recorded in *Conescharellina striata* Silén and *C. japonica* Silén.

The first or primary radicular chamber in a zoarium is always developed on the ancestrula. It differs from the later-formed chambers in that it projects off the basal surface, and has a somewhat rounded outline proximally, rather like the spatulate rostrum of an avicularium. In one fairly young colony, the remains of a chitinous capsule with a fine radicular filament were seen to adhere to the primary chamber. The ancestrula was at first apparently attached directly to a small grain or shell, by means of the capsule, the filamentous thread forming after fixation perhaps when the ancestrula became raised above the substrate.

The sequence of ancestrular budding in this species closely follows that observed by Marcus (1926), and summarized by Harmer (1931: 122) for *Electra pilosa* (Linnaeus) and frequently encountered in other encrusting cheilostomes (Waters 1924: 594). The primary zooecium gives rise to three distal zooecia (text-fig. 1, i) which constitute the first generation. These give rise to the second generation of five zooecia. The developing zoarium is then fan-shaped, but a third generation of thirteen zooecia completely encloses the ancestrula and its early derivatives to form the circular shape of the colony, which then comprises twenty-two zooecia. The zooecia situated proximally to the ancestrula often exhibit some irregularity, and may account for the slight variation in number of zooecia within the third generation

between colonies, e.g., 15 in one specimen (plate 1, fig. 4), due to the interpolation of additional zooecia. On attaining the circular form, new zooecia are budded off from the periphery, thereby raising the apical portion of the colony off the substrate.

The shape of the zoarium in *Australiana bifenestrata*, as in other lunulitiform species, varies significantly according to the degree of maturity. Young zoaria are disc-like structures (plate 1, figs. 2, 3), their basal surfaces being only slightly depressed inwards (fig. 6). The mature colony is typified by its broadly conical shape (plate 1, fig. 1), the central area of the basal surface sloping deeply inwards from the peripheral zooecia (fig. 7).

The structure of the zoarium in *A. bifenestrata* is essentially adapted to a loosely attached mode of life on the sea bottom, anchored by means of the basal radicles. A similar method of attachment is exhibited by *Actisecos pulcher* Harmer (1957: 859).

Zoarial shape in *Australiana bifenestrata* is superficially close to some conescharellinid species, but the Australianidae differ from the Conescharellinidae in several fundamental aspects. These include:—

(a) structure of the zoarium; unilaminar in *Australiana*, with a deeply concave basal surface, whereas in *Conescharellina* the zoarium consists of a solid cone, the interior is filled with a mass of old cancelli, extending to the central area of its base.

(b) orientation of the orifice; this is directed away from the ancestrula in Australianidae, but directed *towards* the ancestrula in the Conescharellinidae, contrary to the arrangement in all other Ascophora.

(c) avicularia; wanting in *Australiana* but proliferated over both the frontal and basal surfaces of the conescharellinid colony.

(d) ovicells; immersed and bifenestrate in the Australianidae (text-fig. 1, b) whereas the brood chambers are hyperstomial and imperforate in the Conescharellinidae.

(e) rootlet chambers; these are confined to the basal surface in *Australiana* while the lunoecia are developed on the frontal surface of the conescharellinid zoarium. The manner in which the latter is oriented with reference to the sea bottom remains in doubt.

Certain features of the Mamilloporidae are close to those of the Australianidae. In *Mamillopora cupula* Smitt, for example, the zoarium is cupuliform, with a concave basal surface. The orifices are also broadly similar, those of ordinary and fertile zooecia being dimorphic, the former with opercular condyles as in *A. bifenestrata*. Nevertheless, such resemblances are outweighed by marked differences, especially the frontal and basal avicularia in *Anoteropora*, a typical member of the Mamilloporidae. Although the ovicells in *Mamillopora cupula* Smitt are immersed (Canu and Bassler 1928: plate 26, fig. 9) they are large, rounded, imperforate chambers as in *Anoteropora magnicapitata* Canu and Bassler. Another difference is the zoarial habit, which is free in both those genera, radicular chambers being wanting.

Some resemblances between the Australianidae and the Actisecidae of Harmer (1957) are evident. The basal surface of *Actisecos pulcher* Harmer has numerous foramina which resemble those of *Australiana bifenestrata*. Rootlet pores with fine filaments " to which minute Foraminifera are attached " (Harmer 1957: 859) also occur on the basal surface of Harmer's species. The long tubular peristomes and the globular, finely perforated globular ovicells of the Actisecidae, however, preclude any relationship between the two families.

Australiana bifenestrata is unquestionably the species MacGillivray (1895: 46) doubtfully attributed to *Lunulites angulopora* Tenison-Woods (= *Conescharellina angulopora*). MacGillivray misoriented his material, which is of a fragmentary nature, interpreting the zooecia as basal avicularia, and the radicular chambers as zooecia. The locality of his material was not given. Waters (1921: 423) commented on MacGillivray's specimens thus: " MacGillivray gives this with a ? as fossil, but it really seems as if both his description and figure have got into the wrong place, at least I cannot understand them ".

Mr. Edmund Gill, Curator of Fossils in the National Museum, Victoria, has examined the specimen in question and he states (*in litt*): " it is labelled 'Muddy Creek'. Presumably it comes from the Miocene 'lower beds' as Polyzoa are rare in the upper beds, and it would be so stated if the specimen came from these ". Gill also confirms, from foraminiferal samples he collected in 1961, that these 'Muddy Creek' beds are of Balcombian, Middle Miocene, age.

ACKNOWLEDGEMENTS

This study was undertaken during the tenure of a post-graduate scholarship awarded by the Australian National University. I am indebted to the Director of the Australian Museum for making the material available for study. My thanks are also due to Mr. E. D. Gill, National Museum, Victoria, for supplying the location of MacGillivray's fossil material.

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EXPLANATION OF PLATE 1

Fig. 1: Mature zoarium. Paratype x 26. Lateral view. A peripheral ovicelled zooecium is indicated. A.M. Cat. No. U.1311. *Thetis* Station 47.

Fig. 2: Juvenile zoarium. Paratype x 26. Lateral view. Sorted from bulk material collected by the *Endeavour* Expedition, off Gabo Island, Victoria.

Fig. 3: Same zoarium as fig. 2, but from a distal-lateral aspect.

Fig. 4: Apical view of zoarium at an intermediate growth stage x 26. *Thetis* Station 47.

Fig. 5: View of the growing margin. Holotype x 28. Ovicelled zooecia encircled. A.M. Cat. No. U.4022. *Thetis* Station 47.

Fig. 6: Basal aspect of an immature zoarium. x 26. The central area is only slightly depressed. Note the foramina. A radicular chamber is indicated. The basal septula on the distal walls of the peripheral zooecia are visible in one or two instances. *Thetis* Station 47.

Fig. 7: Basal surface of mature zooecia. x 26. The medial concavity has become greatly immersed. Focused to show the foramina. *Thetis* Station 47.

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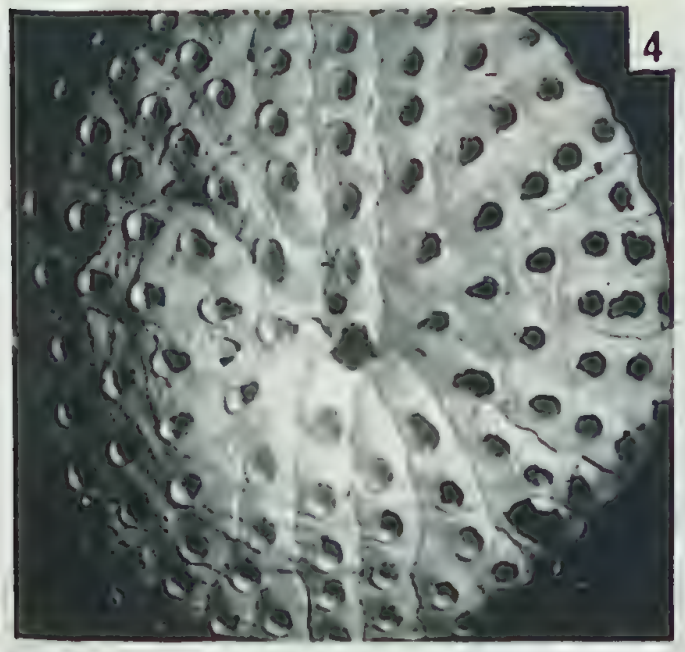
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II. Colony Formation in *Selenaria nitida* Maplestone

ABSTRACT

Selenaria nitida, known only from the Peronian faunal province in Recent seas, is refigured from one of Maplestone's syntypes. Evidence suggests that the New Zealand material that Livingstone (1929) assigned to *S. nitida* Maplestone belongs to *S. squamosa* Tenison-Woods instead. The astogeny of *S. nitida* is discussed, with particular reference to the mode of ancestrular budding, and comparisons are made with *S. cupola* (Tenison-Woods) var. *spiralis* (Chapman) from the Victorian Tertiary. It is considered that this taxon should be given specific status in view of its spiral mode of budding. The budding mechanism in *Selenaria nitida* was found to be substantially similar to that of multiserial encrusting cheilostomes, being initiated by two distal first-generation zooecia which bud off lateral-proximal successors to surround the ancestrula. These zooecia then bud off serially, giving rise to the radial arrangement of zooecia in the adult colony. The same budding mechanism is exhibited by *S. cupola* (Tenison-Woods), another Victorian Tertiary fossil, and also *S. squamosa* Tenison-Woods, an Australasian species.

INTRODUCTION

The writer became aware of the abundance of *Selenaria nitida* Maplestone whilst sorting through bulk collections of Polyzoa dredged by the *Endeavour* Expedition (1909-1914) from 30-50 fathoms off Twofold Bay, New South Wales, and deposited in the Australian Museum.

A check with Maplestone's syntypes (Australian Museum Cat. No. U.196) confirmed the identity of the *Endeavour* material (A.M. Cat. No. E.6802), but revealed substantial differences from fragmentary material from Little Barrier Island, New Zealand (Mortensen Collection A.M. Cat. No. U.2716), which Livingstone (1929: 62) assigned to Maplestone's species. The larger dimensions of the zoarial fragments (Livingstone p. 62) and the zooecia, as well as the elongated opesiae, suggest that Livingstone's specimens should be referred to *S. squamosa* Tenison-Woods instead. (For description and figs. of *S. squamosa* see Brown 1952: 145).

Several juvenile zoaria of *S. nitida* from the *Endeavour* material show various stages of development, and placed in an ontogenological sequence they provide useful information on the early phases of astogeny. Stach (1936: 65, plate 3, figs. 1, 2, text-figs. 1, 3) described in some detail the early stages of colony formation in *S. spiralis* (Chapman) from the Victorian Tertiary. This taxon was formerly regarded as a variety of *S. cupola* (Tenison-Woods). Stach concluded (p. 66) that *S. cupola* exhibited a similar mode of budding. It will be shown, however, that ancestrular budding in Chapman's species is genetically distinct from that in *S. cupola*. Information on a rather different type of budding as demonstrated by *S. nitida* Maplestone is supplied.

SYSTEMATIC DISCUSSION

Genus **Selenaria** Busk, 1854

Type species (by monotypy): *Selenaria maculata* Busk, 1854. Recent: Bass Strait.

Selenaria nitida Maplestone plate 1, figs. 1, 2, 3, 5, 6, 7.

1909 *Selenaria nitida* Maplestone, p. 271, plate 77, fig. 8.

1921 *Selenaria nitida* Maplestone: Waters, p. 407.

Not 1929 *Selenaria nitida* Maplestone: Livingstone, p. 62 (= *S. squamosa* Tenison-Woods).

1952 *Selenaria nitida* Maplestone: Brown, p. 142, text-figs. 87-89. (New Zealand fossil material).

Distribution: (a) Recent: 22 miles east of Port Jackson, N.S.W., 80 fathoms (Maplestone). 30-50 fathoms off Twofold Bay, N.S.W. (*Endeavour* material).

(b) Fossil: Weka Pass (Waiauan, Middle Miocene), New Zealand (Brown).

Remarks: The smaller dimensions of the mature colony of *S. nitida* and of the average size of the individual zooecia, as well as the correspondingly shorter opesiae, are the chief features distinguishing Maplestone's species from *S. squamosa* Tenison-Woods. Furthermore, the basal surface of the colony is flattened in the former species, but concave in the latter. It was not possible to examine all of Livingstone's New Zealand material, but he inferred (p. 62) that the zoaria were larger in size than those of the type material of *S. nitida* Maplestone and would appear therefore to belong to *S. squamosa*.

Maplestone's (1909: plate 77, fig. 8) original figure is so unsatisfactory that it could apply equally well to *S. squamosa*. I have photographed a calcined adult specimen of one of Maplestone's five U.196 syntypes (plate 2, fig. 1) to ensure that his species is clearly established.

Astogeny: Ancestrular budding is evidently established soon after metamorphosis of the larva, for no trace of a solitary ancestrula was found, a point which Lagaaij (1963: 182) also observed in *Cupuladria canariensis* (Busk). The earliest stage represented in the *Endeavour* material is a five-cell zoarium (plate 2, fig. 2), encrusting a fragment of a pelecypod valve. It comprises the ancestrula and a distal and proximal vibraculum, with four zooecia situated distal-laterally. The distal pair abut against the distal-lateral walls of the ancestrula and constitute the first generation [cf. *Cupuladria canariensis* (Busk) Lagaaij 1963: text-fig. 10b]. The adjacent pair appear to have been budded laterally from these and are to be interpreted as the second generation. Brown (1952: text-figs. 93, 94) figured an identical juvenile zoarium in *S. squamosa* Tenison-Woods, and erroneously considered (p. 147) that all four zooecia were directly produced from the ancestrula. The juvenile fan-shaped colony is bilaterally symmetrical in both *S. nitida* and *S. squamosa* and a prominent fold of tissue or basal kenozooecium (Brown 1952, caption to text-fig. 93) is exposed along the proximal margin over which the third generation, budded off from the preceding pair, is later formed. A further pair, i.e., fourth generation, is budded from the third generation zooecia to complete the circlet of zooecia around the ancestrula (plate 2, fig. 5).

To summarize: Colony formation in *S. nitida* is initiated by two first-generation zooecia, the right member budding off clockwise lateroproximally, while the left member buds in an anti-clockwise direction, thereby establishing a circlet of eight periancestrular zooecia.

I should like to emphasize that the development of the periancestrular zooecia has not been directly observed. It is well established, however, that not all the several zooecia surrounding the ancestrula in the multi-serial cheilostomes are produced as its buds (Harmer 1931: 159, 160).

Confirmation of this is provided by *Electra pilosa* (Linnaeus), an encrusting cheilostome, whose budding mechanism has been studied by Waters (1924) and Marcus (1926), and summarized by Harmer (1931: 122). Here three distal buds arise from the ancestrula, representing the first generation of zooecia. Successive generations are budded off distally, forming the young fan-shaped colony, the distal-lateral edges of which are soon reflected proximally and meet on the proximal margin of the ancestrula. The writer (in part I of these studies) has documented a closely

similar budding pattern in the new ascophoran *Australiana bifenestrata* from south east Australia. As Harmer (p. 162) noted, the actual number of zooecia surrounding the ancestrula is not constant for a species. In *S. nitida*, for example, it may vary from seven to nine.

I have examined a juvenile colony of *S. spiralis* (Chapman) from Caldwell's Cliff, south-west Victoria (Pliocene) (plate 2, fig. 4). This fossil specimen is of particular interest because the stage of development is almost equivalent to that of *S. nitida* (plate 2, fig. 3), except that both fourth-generation zooecia are wanting. Useful comparisons can, however, be drawn between the two.

Stach (1936: 65) has shown that budding in *S. spiralis* (Chapman) is initiated simultaneously from the right side of the distal half of the ancestrula as well as the left side of its proximal half to form two first-generation zooecia, and three successive pairs are budded off in a clockwise direction laterally. The fourth pair (i.e., B4, A4 components in Stach's terminology), normally situated at the distal and proximal margins of the ancestrula, are not developed in the present fossil specimen (plate 2, fig. 4) and its symmetry at this stage is analogous to the two-fold crystallographic symmetry axis.

Essentially the budding mechanism in *S. nitida* and *S. spiralis* is the same in that the eight zooecia surrounding the ancestrular region are formed by the budding of two first-generation zooecia. The important difference concerns the spiral mode of budding in the latter species, resulting from the oblique position of the two first-generation components both of which bud off laterally in a clockwise direction (plate 2, fig. 4).

Once the circlet of zooecia is completed, further budding in *S. nitida* commences from the two first-generation zooecia, each of which produces one distal successor (plate 2, fig. 5). Budding is then initiated from the lateral and proximal margins as well, until the circular outline of the colony is attained (plate 2, fig. 6). A tendency towards radial growth now becomes apparent (plate 2, figs. 6, 7), the semi-mature colony having eight primary rows, corresponding to the number of zooecia encircling the ancestrula. The secondary branches, however, are established between these when some members of the circlet bud off two distal successors. During later stages of development (plate 2, fig. 1), new branches are intercalated when space permits.

Discussion: Stach (1936: 66, text-figs. 2, 4, 5, 6) considered that the ancestrular region of *S. cupola* from the Victorian Tertiary showed spiral development similar to *S. spiralis*. Careful examination of the photograph of the plesiotype from the "*Glycimeris* Beds" (Stach: plate 3, fig. 3) which appears to correspond to his figured specimen (i.e., text-fig. 2; the magnified ancestrular region in fig. 4 seems to have been taken from a different specimen), does not substantiate Stach's opinion. The periancestrula zooecia are bilaterally symmetrical as in *S. nitida* (fig. 5), and comprise two distal, four medial and two proximal members; the B4 components at the extremity of the distal vibraculum in Stach's text-figs. 2, and probably also in 4 and 5, are not analogous to the fourth-generation component in *S. spiralis* as it is budded from either the left or right first-generation zooecium proximally. The A4 component, positioned in Stach's figure 2, at the extremity of the proximal vibraculum is misplaced; it does not abut on the distal wall of the vibraculum as shown, but is situated to one side of it and comprises one of the members of the proximal or fourth-generation pair as in *S. nitida* (plate 2, fig. 5). Through the kindness of Professor M. F. Glaessner, Geology Department, University of Adelaide, I was able to examine the syntypic material of *S. cupola* (Tension-Woods) from Muddy Creek (Middle Miocene). Only in syntype G (Stach, text-fig. 6) is the apical region intact, and the periancestrula zooecia show the same orientation as in plate 3, fig. 3 of Stach.

From the foregoing observation it follows that the mode of budding in *S. cupola* is not the same as in *S. spiralis* as Stach maintained, but is allied to *S. nitida* instead. It now becomes evident that the important difference between *S. cupola* (Tenison-Woods) and *S. spiralis* (Chapman) is the radial growth of the former species built up from the serial budding of eight zooecia, in contrast to the spiral growth in the latter, which is initiated by the clockwise budding of two first-generation zooecia, and continued as two spiral whorls. Clearly, the mode of budding in Chapman's species constitutes an important genetic distinction.

Conclusions: The maintenance of strict bilateral symmetry during the earliest stages of colony formation in *S. nitida* and radial growth during the later stages of development achieves an even disposition of zooecia within the colony, demanded presumably by the feeding requirements of the individual polypides, as well as the need to preserve the equilibrium of the colony in its free mode of life.

Some lunulitiform species attain their equilibria by developing spiral growth; these are *Heliodoma implicata* Calvet, *Setosellina goësi* (Silén), *Setosella spiralis* Silén and *Selenaria spiralis* (Chapman). The phenomenon of spiral growth has received particular attention by Silén (1942). He has shown that the spiral series may either be derived from two first-generation buds as in *Heliodoma* (and demonstrated by Stach for *Selenaria spiralis*), or as in *Setosella spiralis*, where either one or two spiral series are formed; the second series is derived from the bifurcation of the single first-generation bud and not from the ancestrula. In some of the species, however, which Silén used to demonstrate spiral growth, e.g., *Setosella constricta* Harmer and *Setosella vulnerata* Busk, the zooecia often bifurcate during budding and concentric spiral whorls are not developed. Lagaaij (1963: 182, 184) has also shown that Silén's theory of spiral growth is not valid for *Cupuladria*.

ACKNOWLEDGEMENTS

This study was undertaken during the tenure of a post-graduate scholarship awarded by the Australian National University.

I am indebted to the Director of the Australian Museum for making the material of *Selenaria nitida* Maplestone available for study; also Professor D. A. Brown, Geology Department, School of General Studies, Australian National University for permission to examine his collection of fossil Victorian Polyzoa.

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EXPLANATION OF PLATE 2

Fig. 1: *Selenaria nitida* Maplestone Syntype x 30. A.M. Cat. No. U.196. Locality: 22 miles East of Port Jackson, 80 fathoms. Mature colony.

Fig. 2: *Selenaria nitida* Maplestone x 30. Five-cell zoarium. Comprising the median ancestrula with distal and proximal vibraculum and two first-generation zooecia distally, each of which has budded off a second-generation zooecium laterally (cf. Brown 1952, text-fig. 93, *S. squamosa* Tenison-Woods).

Fig. 3: *Selenaria nitida* Maplestone x 30. Eight-cell zoarium. One fourth-generation zooecium is yet to be intercalated at the proximal margin.

Fig. 4: *Selenaria spiralis* (Chapman) x 30. Locality: Caldwell's Cliff, South West Victoria (Pliocene), Brown Collection. Seven-cell zoarium. This stage is almost equivalent to fig. 3. Note, however, that the zooecia are budded off in two discrete series resulting in the formation of double spiral whorls in the mature colony (Stach 1936, text-fig. 1).

Fig. 5: *Selenaria nitida* Maplestone x 30. The circlet of zooecia around the ancestrula is complete and the two first-generation zooecia have commenced serial budding distally.

Fig. 6: *Selenaria nitida* Maplestone x 30. Budding is well advanced on the distal margin of the colony, less so laterally and proximally. Note the incipient radiate growth.

Fig. 7: *Selenaria nitida* Maplestone x 30. The semi-mature colony has attained its circular shape. (Figs. 2, 3, 5-7 all from A.M. Cat. No. E.6802, off Twofold Bay, N.S.W.)

Sydney: V. C. N. Blight, Government Printer—1966

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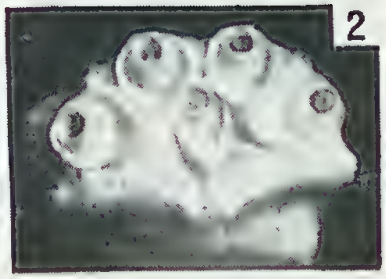
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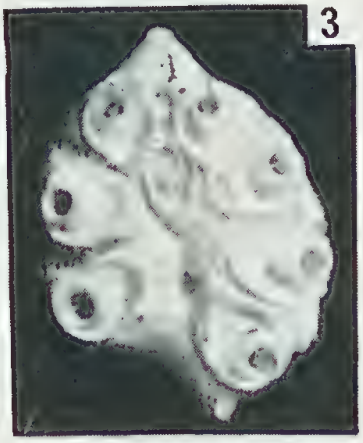
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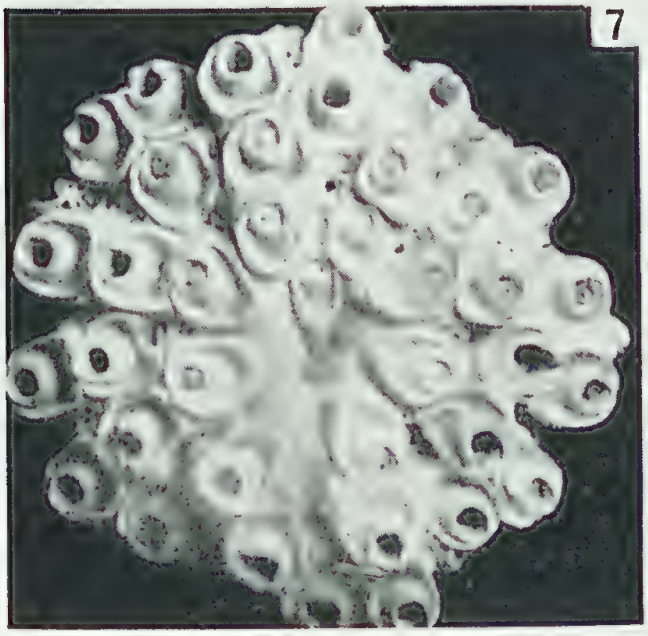
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5

A STUDY OF BUKA-PASSAGE (SOLOMON ISLANDS) CEREMONIAL PADDLES

By H. Spiegel

Plates 3-15. Figs 1 and 2. Manuscript received, 5th November, 1964.

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PREFACE

It has been a very rich and rewarding experience for me, as an art-historian, to be able to do research in the field of the Solomon Islands ceremonial paddles.

My main concern was with the stylistic features of the paddles, their shapes and the specific motifs of their decoration and, to a lesser degree, with the meaning of patterns and their significance. I tried to trace the distribution of the different motifs, especially the motifs of the squatting ancestor figure in the position of adoration in the Pacific area and to draw some conclusions purely from the facts which I could establish and which might be confirmed by the findings of anthropologists.

I do not claim to have given a fully comprehensive account, as one has naturally to rely on literature and studies done so far by other scientists about the art and culture of the different island groups, but I hope this paper will serve as a basis for further research and, if I have achieved this, I will feel very satisfied.

My thanks for being able to do this work go first of all to Mr F. D. McCarthy, former Curator of Anthropology at the Australian Museum in Sydney, who suggested this subject to me and who was always a very helpful adviser in all questions of doubt. I am also indebted to the former Director of the Museum, Dr J. W. Evans, the Librarian, Miss M. Davies, and members of the staff who were always ready to give me their assistance.

INTRODUCTION

The large number of paddles (approximately 320), which are part of the excellent collection of objects from the Solomon Islands, were bought by the Australian Museum in Sydney in two big parcels, according to the register of the Museum, from Richard Parkinson and Captain Farrell in 1885 and 1898 respectively. The paddles are described as coming from the Buka district.

Richard Parkinson, author of the well-known book "Dreissig Jahre in der Suedsee" (Stuttgart, 1907) and many other valuable contributions to the investigations of the peoples, life and culture of the Pacific Islands, was the brother-in-law of Captain Farrell and both were related to "Queen Emma", a famous trading woman, who lived around 1880 in Rabaul.[1]

This evidence shows that the paddles from the Buka district were made previous to 1885 or 1898 at the latest, when the Solomon Islanders were still more or less in their primitive state and had little contact with the white man. We therefore can look upon them as authentic specimens and products of the art expression of the Buka-Passage Islanders, inspired by the feelings and the spiritual background of their time.

The paddles are identified by their registration numbers, which are quoted in the text.

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[1] According to information received from Captain Brett Hilder, Sydney.

1. THE GROUPING OF THE BUKA-PASSAGE PADDLES

The paddles and wands in the large collection of the Australian Museum can be divided into three different groups, according to their shape and their decoration, which are rather closely connected with the different types. One motif which is common to all groups is the Kokorra motif, the human figure with a very big head, large eyes, wide nose, a dome-shaped hair-do, shells above the ears which are always long and decorative and end in a specific shape. The body of this figure is more or less elongated, the arms are raised in a position of adoration with the fingers sometimes touching the ears, and the legs are in a squatting position, whilst the feet may be turned inside or outside. The head of this spirit appears often without a body, or the body might be shown in profile and in an upright position. (Kokorra is the name given to this specific figure, an ancestor figure in the Buka district related to the korwar figure typical of north-west New Guinea which has given its name to the so-called "korwar style.")

Most Buka paddles and wands are decorated with geometric ornaments beside the kokorra motif and some show zoomorphic motifs such as birds, fish or other animals as well. There are a few which show geometric ornaments only, or predominantly geometric ornaments, sometimes in connection with floral motifs.

Technique

The decoration of all the paddles is executed in the same way with the exception of those from group II, where the flat relief, in which the ornaments are carved, changes into fully sculptured spirit heads at the end, whilst the blades are plain or show the same patterns as the other paddles. Most paddles and wands are painted but there are many unpainted paddles which would eventually have been painted. A great number of wands, most of which belong to group III, are carved and afterwards stained in sepia on the ornamented parts, whilst the ground remains in the original light natural colour. It is possible that the paint is applied on top of the stain, as some paddles are partly stained and partly painted. The examples which are stained only are much more refined than the more primitive and crude-looking painted ones. Exceptions are some of the hardwood paddles which show traces of paint only on the ornamented parts, whilst the ground which is otherwise painted white remains polished wood. The great majority of the wands are carved from softwood but the paddles (group I) are made from heavier wood.

Once the shape of the paddle or wand was decided, the design was outlined with a sharp instrument and the surrounding ground carved away, so that the design stands out in a flat relief, approximately one-eight of an inch in height. The outline is more or less finely or crudely done, but the wands show a remarkable degree of skill, a sensitive line and a notable sense of artistic feeling in filling the available space.

Material and tools

The material of which the wands are made is mostly softwood, though fairly hard wood was used for canoes. In Petats, a village on Buka Island, the wood used comes from a tree called "uertsil"; in the village of Kuratschi, on the north coast of Bougainville Island, it is called "tfinio". This is a tall slender tree with smooth bark which strips off in large slabs. The wood is white and so soft that one man can fell a "tfinio" by himself, unless it is a very large one. (Blackwood, 1935, pp. 362-3.) For the construction of rafts, and of the "mon", a canoe built from planks, the wood of the so-called "panots" tree is used. A large tree will provide five or six planks for a medium-sized mon. (Blackwood, 1935, p. 371.) There are also huge trees with enormous flanges buttressing their trunks and the aerial roots of the banyan which

might be used for paddles. (Blackwood, 1935, p. 11.) Bernatzik (1936, p. 81) reports that mostly softwoods are used on Owaraha, an island belonging to the south-eastern group of the Solomons. The wood there is called "taba" and is resistant to termites and borers.

Parkinson (1907, pp. 289, 327, 500) reports that in the Admiralty, the Bismark and the Solomon Islands various species of the bread-fruit tree are used for canoe building. The wood is light brown in colour and light in weight.

In the olden days, the most important tool was the adze with a blade made from stone, a piece of coral, the shell of the tridacna, the hippopus or the terabra snail. Knives were made from obsidian. The teeth of pigs or dogs were used for cutting the outlines. For smoothing down surfaces a scraper made from oyster or mother-of-pearl shell and a sharkskin, respectively, were used. Drills on Buka Island were fitted with a piece of quartz as a point. Painting brushes were made with cocos fibres. Fine sand or pumice were used for polishing.

Most paddles and wands were painted in white ground colours and in red and black on the carved ornamentation. The white was produced by rubbing the surface with the seaweed "ino", a calcareous algae. A handful of seaweed was freshly gathered from the reef, and without further preparation, rubbed over the wood.

The several kinds of red paint are varieties of oxide of iron formed in the neighbourhood of volcanoes. There is a bright red, a muddy one, and a colour between these two.

Black may be obtained from volcanic ashes or by mixing charcoal with oil (Blackwood, 1935, pp. 416-7).[2]

Use of paddles and wands

Very little is found in the literature about the use of ceremonial wands, especially the very large ones, which were apparently not used for transportation. The paddles of group I are of a type commonly used in the dug-out and plank canoes in the different groups of islands in the Pacific Ocean. These paddles may be plain or decorated and the latter ones are used with the decoration facing the paddler. (See B. Blackwood, pl. 49, and R. Parkinson, pl. 29, p. 510.)

Guppy (1895, p. 74) mentions that some men were seen carrying clubs in their hands which could be used for paddling as well as a weapon, being heavy and strong. Their name—paddle-clubs—already points in this direction. Most clubs are pointed at the butt-end to enable them to be struck upright in the ground. "These weapons are rarely seen in the hands of the natives of Bougainville Straits, if I may except an ornamented club which is carried at dances," Guppy writes. "Some of these ornamented clubs exactly resemble, both in form and decoration, some clubs from New Ireland in the British Museum".

Godrington (1891, 306) mentions that "in Florida and thereabout a paddle-shaped club is a favourite walking weapon called *rau ni Aba*, Aba being a place on Guadalcanal Island, where they are made."

Parkinson[3] (1907, p. 481) mentions that clubs, made from light-weight wood painted and carved, were used at the ceremonial dances taking place at a chieftain's wedding. He shows further, on p. 649, pl. 122, the picture of a wooden carving from

[2] Nothing is said about the stained paddles.

[3] Parkinson calls a dancing-club what I call a ceremonial wand, according to the illustration on p. 560, pl. 36.

New Ireland, representing a boat with four standing figures of demons in it, carrying in their right hand a kind of paddle or paddle-club.

There exist also very small paddles, and paddle-shaped dancing sticks, used by women, which obviously were not used for paddling canoes.

It is obvious that the paddles had various uses, from the most simple shapes employed for transportation only, to the more refined and decorated ones, used in ceremonies and as weapons as well. It is understandable that a paddle could be used as a weapon and that a man who had to carry a paddle and a spear would have the need to make use of the paddle as a club, also as a shield, and that eventually he combined these usages in the shape of a paddle-club.

The ceremonial uses of paddles are very varied, as the paddles played a big part in the life of the natives of the islands. Being such important objects of everyday life, paddles were put into the graves and buried with their owners (Hambruch-Eilers, 1932, Ponape 2. Teilbd p. 91 and also p. 203 and 210) together with weaving implements, cocos and banana leaves, pipes, necklets, loin cloth and other objects, in the belief that the dead would need all these objects in their life after death. Hambruch-Eilers also report that on Ponape Island (East Carolines) dancing paddles are specially precious objects, carved from the wood of the bread-fruit tree and used at paddle dances performed in the presence of the chieftain at the boat consecration ceremonies. These paddles had a wide and flat blade which was painted black, whilst the carved design was painted white. These paddles were also put in the graves with the dead. A number of paddle-songs were sung at these ceremonies.

It is reported from Palau (West Carolines) by A. Kraemer that dancers had different objects in their hands while performing ceremonial dances, such as spears, models of fish, branches and paddles. The latter were called dancing paddles to distinguish them from the ones used for paddling canoes, and were decorated with carved designs painted red or blue.[4] (Kraemer, 1932, Bd. 3, Tbd. 3, p. 182, fig. 164, and p. 318, fig. 211 and pl. 16.)

Blackwood (1935, p. 189) reports that at dances performed by women when a male child was put on the pack for the first time, carried by his mother on her back, the women carried fish-nets, bows and arrows, axes and paddles in their hands, all objects symbolic of a man's activity; in the case of a girl the paddles would have been used too, as women as well as men are expert paddlers.

Clans of Buka and of North Bougainville

It will be necessary to examine the social and ritual inspiration of some of the main motifs which are to be seen on the paddles, particularly the anthropomorphic creatures and animals, which are sometimes combined to form fantastic beings. It will be well to examine the possibility of a totemic origin of these motifs. B. Blackwood said: "On the island of Buka and its adjacent islets there are, in general, only two clans represented at the present time. They are called over most of the island, Naboin and Nakarib, the same as the two chief clans on Bougainville. But, on Petats and some of the other islands they are always referred to by the name of the birds associated with them, Manu being invariably substituted for Naboin and Kekeleo for Nakarib. Manu seems certainly to indicate an eagle, whilst the meaning of Kekeleo was not so easily defined. Kekeleo is a somewhat vague term, which might be translated 'fowl', while applied primarily to the bush-fowl or megapode; in some

[4] Miss E. Pope, of the Australian Museum, was so kind as to draw my attention to dances performed on 14th July, 1960, on Wallis Island (New Caledonia), where the male dancers used blue and red painted paddles at their dances.

districts on the east coast however the term might indicate a fish-hawk". And on p. 35: "On the north coast the list of clans varies slightly in different villages. I give all those that come to my notice passing along the coast from west to east". (Saposa, Tabut, Ruri, Hahon district, Kurtatschi, Baniu and Tiop.) According to her list the associated totems are the eagle for the Naboin clan and the hawk for the Nakarib clan, whilst for the numerous other clans in this district, birds named are the hornbill, red parrot, white cockatoo, black gull, the megapode and several other small species. There are also mentioned the dog, possum, tree-rat, crocodile and turtle.

Origin of clans and totems

Blackwood writes (1935, p. 37): "It does not seem to be thought that the people are descended from the creature whose name is associated with their clan. The origin myth is the same, with local variations throughout the area, and the same myth is also widespread in other parts of Melanesia". According to this myth, a woman was left behind on the seashore when all the people fled in their canoes before a terrible monster or spirit, or some giant. Left alone she copulates with a banana and in due time bears two sons, who, when fully grown, kill the monster. When this becomes known the people return, and two girls marry the two brothers. From these two couples all the people are descended. In one version obtained from the village of Kohiso in the hill district of central Buka, the end of the story is that the two brothers turned into birds, but the kind of bird is not specified. Page 4: "In the conditions obtaining in this area in regard to totemism (if it is called totemism) we find the following state of affairs prevailing. The people are divided into groups each having a certain relationship to a species animate or inanimate, which is of the same general kind for each group, and a member of one of these totemic groups cannot (except under special circumstances, such as adoption) change his membership. This is a minimum definition of totemism in the wide use of the term. The totemic species is not regarded as an ancestor. There is also lacking the idea that the associated creature ever helps the human being belonging to the clan. In former times a man would not kill the creature of his clan, but a member of another clan might kill it without arousing his anger. These conditions have prevailed in the last three generations and seem not to have been brought about by the influence of the contact with white people".

Now, in which way are these facts connected with the decoration of the paddles and wands? It seems quite clear that the designs are connected with the totemic symbols of the different clans and that the wide variety of patterns is in accordance with the relationship of the different groups of people to a species, animate or inanimate, which is of the same kind for each group. Examples of these social relationships are seen in group II where tatoo patterns are used as decoration, and where different colours (black and red) are used in painting the hair-do of the kokorras.

There is no special mention of lizards, bonito, or sharks as totemic animals, although they play an important part in the decoration, and, of course, in the life of the islanders.

Kokorra

The most important motif is the kokorra (B. Blackwood, 1935, p. 435), a squatting figure with raised arms used as decoration on paddles, boats, musical instruments (the "mabu"), wind instruments, and on slip-gongs, used at ceremonial and social dances. Kokorras simply means "man". In the Ruri district (north-west Bougainville) another explanation given in pidgin-English of this anthropomorphic

figure was "all same Father call em God". All authors mentioning this figure speak of it as a demon or spirit. The foremost spirit in Buka and its surroundings is the spirit of the dead called "urar". A person turns into an urar after death and joins his dead clansmen who also turn urar. The meaning of all death ceremonies is to satisfy these spirits by offering them food and doing honour to the dead person, in order to pacify the spirit so that it may not haunt the place of the deceased's former abode and disturb his relatives and clansmen. During the time it takes to change into an urar all kinds of taboos are enforced on the relatives, such as special eating habits, women may not wash themselves, wear a special belt, and have to live in seclusion until the final feast, when the dead is buried and all restrictions are removed.

The urars play an important part in the lives of the islanders and many tales are connected with them. The urars are invisible to men, but the animals sense them; they can make themselves visible to humans, are believed to be able to assume any disguise and change into any shape, animal or person. (B. Blackwood, 1935, p. 483, "Death and the Urar".) On page 522 she writes: "Those to whom they appear do not recognize them as urar, till some untoward happening in their relationship with the animal or fish or bird in question opens their eyes to the true character of the being with which they have to do." R. Parkinson (1907, pp. 650-1) mentions that carvings in New Ireland are representations of pigs, sharks, serpents, dolphins and lizards, naturalistically represented; they are not totem animals but evil spirits which fight with the manu but eventually get subdued.

What, now, is the relationship between a kokorra and an urar? Having noted that the kokorra is by some islanders described as a man and by others as a kind of God or spirit, might it not be possible that the kokorra called a "man" and showing quite naturalistic features, in contrast to the more a-naturalistic, typified kokorra, is an urar in disguise turned into a "man".

If the numerous representations of fish, sharks, lizards with Kokorra-heads are not totemic symbols, they might be urars which have taken on these different shapes.[5]

That the special, typified representations of the demon or spirit which I call kokorra with the arms raised is not the representation of an ordinary human being is proved by the wide distribution of this motif all over the islands of the Southern Hemisphere. (Lommel, 1962, shows the occurrence of this motif and its derivations in all kinds of material with the different peoples.) Besides the figure with the raised arms is a well-known type identified with the "Orantes" of other religions. And where does the motif of the double-headed, Janus-type kokorra come from? With these questions in mind we can now turn to the description of paddles and wands.

Group I. Paddles

This type of paddle is the most widely used in the Pacific area. It is found in New Guinea and in most of the Islands either in its decorated or plain form, made from different kinds of wood. The paddles from group I are much heavier than from other groups. They are carved in one piece and the lancet-shaped blade is approximately of the same length as the handle. The average length of the blade

[5] Ivens (1927, p. 137) reports from Ulawa: "The magical control of the bonito was considered to lie in the power of ghost-sharks and sea spirits. The ghost-sharks were incarnations of men who, during their life-time, had manifested their power by being successful in the bonito catching. At Sa'a the bodies of such men were exposed for burial in a canoe on the beach, and their skulls and jaw bones were preserved in a special shrine alongside the canoe-house being enclosed in a wooden figure of a swordfish. At Ulawa the skulls of those who were to become shark incarnations were placed on rocks. Such shark-ghost when prayed to came up to the canoe and brought the bonito in their wake".

is between 32 and 34 inches, the width of the blade also showing slight variation-from 6 to 8½ inches. Sometimes a crutch is added to the handle, sometimes the handle is continued as a rib onto the blade. (Bodrogi, 1959, pl. 116; Linton and Wingert, 1946, pp. 179, 184; Buehler, Barrow and Mountford, 1962; Schmalenbach, 1956, pl. 13 and 15, Blackwood, 1935, pl. 49.) (Pl. 3).

The Kokorra motif

The motif most frequently used on these paddles is the head or the whole body of the spirit called kokorra. Slight variations occur on each paddle and no two are alike. Sometimes both sides of the blade are identical, sometimes the colours are reversed. On some paddles only one side is decorated, others again show different motifs on each side. The kokorra heads or whole figures are sometimes shown pointing with their heads towards the point of the blade, but they might face in the opposite direction as well.

The full figure is the most widely used motif on all groups of paddles and wands and the most characteristic one for the Solomon Islands, especially those from the Buka district. These conventionalized human figures and faces have the same features, namely a large dome-shaped hair-do separated from the face itself by a distinct line, big circular eyes, under a feature which is slightly differentiated with each face, consisting of eyebrows, forehead and nose in one piece (reminescent of the body of the sea-eagle on some paddles), a mouth with or without teeth, and a wide chin; joined on to the head are always two shell-like features, and, underneath these, very elongated ears ending mostly in a leaf-like or drop-shaped ornament. The body of the spirit is, in general, always in the same style, that of a squatting or sitting figure with knees drawn up, arms raised and almost touching the elongated ears. In this design the arms form the letter W and the legs the letter M, the body is more or less thinly drawn out, and the arms and legs are slender, with emphasis on shoulders and buttocks. The head is mostly larger than the body or at least quite as big, a feature of Oceanic sculpture. There are frequently no fingers, just a widening on the ends of the arms; four fingers may be indicated and rarely five. The feet are either turned inside or outside, rarely indicating toes. The great majority of kokorra representations are similar, with some slight and some exceptional variations.

The large dome-shaped hair-do is sometimes rounded at the top, but is mostly onion-shaped. It is painted red or black, or sometimes half black and half red, sometimes divided in the centre by a lozenge in red or black. This centre piece of a different colour might correspond to a practice recorded by Blackwood (1935, p. 149). It indicates the grade of naturalism which is included in the otherwise schematized shapes of the kokorras. According to Blackwood the hair-do is trimmed round the temples and across the forehead in a special line. A line of white paint usually follows the edge of the hair-do. On special occasions a pattern in black or red is painted on the hair according to the clan of the individual. Members of the Naboin clan paint the sides black with a wide band of red in the centre, passing from front to back. Blackwood (1935, pl. 66) has a photograph of a young dandy with shell ornaments above the ears and dome-shaped hair-do. There is no difference between the male and female hair-do's of carved figures used in certain ceremonies (Watawut ceremony, Blackwood, 1935, pl. 28); the kokorra heads are similar in this respect.

One very characteristic feature of the paddles belonging to group I is that the blades are relatively empty in comparison to the wands, on which the whole available space is decorated. Another very characteristic feature is a stand on which

the heads of the kokorra are mounted. These stands are in a variety of shapes, from the simplest rib-like stand growing out of the blade where it is thinning to form the handle to quite complicated features (see fig. 1) reminiscent of a sort of simplified spirit's body, as on the wands. Some of these stands resemble birds. Frequently a wing-like or crab-like ornament is also used to fill in the empty space (fig. 1). These ornaments are called "ku a poits"[6] and seem to be the claws of a large salt-water crab, which are used as ornaments at dances.

The whole spirit, i.e., head and body, is also used as a decoration on the paddles, sometimes in combination with another head, but not so frequently as on the wands (pl. 3).

The second most frequent type of ornament in this group is the bird motif. Here again there is no rule to be observed, as the bird may be shown soaring up towards the point of the blade or pointing towards the handle, either looking to the right or to the left. These birds display a remarkable degree of naturalism in their design, in which the most characteristic features of the sea-eagle are represented—the large beak, small head, curved downward-pointing wings and the spread tail. The head is shown in profile, the body from underneath or above. To make the composition look more awe-inspiring two large circular spots, like eyes, are sometimes featured on the body. Some of these birds also appear to be sitting on stands. The plumage is quite strikingly represented (E 1159, pl. 3). The birds are painted in white, black and red, with an effective use of the white ground colour of the paddle blade, from which the ornament of the bird's plumage stands out as in filigree. Some paddles are decorated with a stand only (E 1151, E 1145 and others); some show only the median rib (E 7915).

By comparing the different motifs of this group, we gain an insight into the working of the mind of the native artist. If one presumes that the artist observed the birds perching on a tree or pole and had used that motif for decoration, one might consider that he used also the spirit's head on a stand—as both bird and spirit's head are symbols and equally often used in this connection. Spirit heads are shown on stands which resemble birds, with the feathery wing or crab-claw motif—or derivation of birds and sometimes even a bird which would mean a fusion of both motifs; it might also indicate a fish (E 7928 and B 7855). In any case these stands are a very puzzling feature. The heraldic birds on stands might be identical with the soul-bird, so often seen in Indonesian burial representation.

On another paddle, the fusion of both symbols might be best observed in an elaborate ornament, derived from the middle feature of the spirit's head, comprising the nose, eyebrows and a kind of centre-piece decoration on the forehead, which in itself resembles a bird in conjunction with the wing or crab motif (B 739). Sometimes two circles as eyes are added. It is hard to say whether this centre piece just by chance resembles a bird, or if it is intentionally designed in the shape of a bird; I think the latter is the case. These wing-motifs in alternating colours of red and black possess highly decorative effect (fig. 1).

Although the paddles in group I have a characteristic shape and range of motives related to the shape of the blade, some paddles in this group posses a style of decoration which links them with other groups. They thus form a transition type which illustrates the uniform character of Buka district art, in spite of major differences between the groups and their decoration. The spirit's head with the triangular body or stand shows some features represented in the other groups. These

[6] Blackwood, 1935, p. 433; Nevermann, 1933, shows the claw of the squilla crab of St Mathias used as a necklet.

triangular bodies are filled with a zig-zag ornament, which can as well be basically related to teeth or scales or feathers.

Exceptions of group I

Although the greater part of the blades of these paddles is undecorated there are exceptional paddles on which the whole of the blade is filled with decoration. This decoration includes motifs of different kinds, beside the bird symbol, and the handle is differently shaped, pointing in this way towards group III.

All paddles discussed so far showed the kokorra in full frontal view, and there are few exceptions to this practice. Paddle B 725 shows a whole kokorra head from the front, and the body in profile, with one arm only, raised in the usual way, and one leg only, sitting on a simple stand, growing out of an ornament which marks the junction of the blade and the handle.[7] We will see later on that the figure of the kokorra in profile is quite frequently used in group III, whilst it is an exception in group I. Another exception is paddle B 738 which shows, on one side of the blade, four animals in pairs in profile opposite each other, standing, so to say, on the middle rib extending from the handle (pl. 3). These animals are unique; they are the only ones of their kind which represent pigs or dogs in a rather naturalistic way. They are carved in flat relief on a white painted ground and the bodies are covered with red and black paint. There is only one paddle (B 8722) decorated with a bird in profile; its body is covered with zig-zag lines, which may indicate feathers or scales (pl. 3). There is, however, a paddle in the British Museum showing two similar birds in profile standing opposite each other.

Group II. Wands

This is the smallest of the groups, as there are only about 38 examples of this kind in the collection. They are characterized by their overall shape and special kind of decoration. They consist of a pointed oval blade, with wide shoulders, thinning into a decorated and carved handle averaging about 42 inches; they range from about 39 to 82 inches. The width of the blade is between 5 and 9 inches.

The material is a light softwood quite unsuitable for any practical work and there is no doubt that these paddle-shaped objects were used for ceremonial purposes only. Their most characteristic feature, however, is the handle carved into a fully sculptured but stylized kokorra head, or, as in most cases, a double head, like the Janus head in Greek mythology, showing two faces under one fully carved hair-do with a thin halo-shaped flat feature on the top. (B 8921, pl. 5.) Some examples have one head carved in a more naturalistic manner. The carved double or single heads measure from 2 to 4 inches across the widest part. The features of the face are carved in the usual low relief and painted red or black, or red and black on a white ground.

As with all the other paddles no two are alike and the faces show quite distinct differences in spite of many common features. The nose never protrudes, but is indicated by a flat incision in the same way as the lips and mouth when viewed from the side, and the big eyes are always circular. (B 8921, B 8752 on pl. 5.) The chin may be pointed or slightly rounded, but on the whole the majority of faces are thin, longish and a-naturalistic. This type of face is mostly accompanied by the thin halo-like or onion-shaped feature on top of the hair-do. A ridge runs down

[7] Reichard, 1933, II, pl. CLI, 638b, shows a kokorra in side view carrying an axe on a paddle of group I.

from the hair-do to the chin, giving the head a cubistic kind of appearance. The onion-shaped halos are mostly painted white and the colours of the faces underneath are black and red, usually reversed on the two faces. The ground colour is white on the faces, and this gives them a mask-like expression.

On a second type the hair-do or halo is more or less a continuation of the face. The face is wide and more naturalistic, the hair-do is more pointed and mostly decorated with flanges of different colours. The flanges might indicate the habit of colouring the air in red and white, indicating the clan to which the native belongs. (Blackwood, 1935, p. 149.) (See pl. 5, B 8905.)

There are three exceptions to the two above types; one is a single-headed paddle and the other two are double-headed, which show no features beside the eyes, but the whole face is covered with a pattern of lines, reminiscent of the tattooing of faces in Maori fashion,[8] executed in slight relief. The heads are covered with a slightly elongated ball-like headgear, rounded off at the top, decorated with flanges in red and black in one (pl. 4, E 16513) and plain in the other two examples.

One feature, common to all kokorra heads, is the elongated ear ending in a kind of ornament, under a small protrusion, carved in the round and touching the shoulders of the flat portion underneath the head. This ornamented flat area could be described as a body, although it has nothing to do with the spirit's body proper, as we know it from examples previously described. A short neck leads from the head or heads to that part of the paddle which continues into the blade. This decorated part forms a unity with the head, an arrangement which is completely different to that of the full-figured kokorras on the paddles of group I. In three specimens the usual kokorra body is carved in filigree underneath the double-head (pl. 4, B 8905, B 8740 and B 721). In all other examples there is a special ornamented zone joined to the head by a neck and by the elongated ears reaching down from the head to touch the shoulders. The great majority of specimens follow the same pattern, bearing a purely linear-geometric design on this portion, mostly consisting of parallel concentric lines, repeating the same motif several times. (B 8921, B 8916, B 8940 and B 8907.) The nape below the neck is usually decorated with a necklet, consisting of 1,2, or 3 lines of zig-zags sometimes associated with a voluted ornament (pl. 4, E 16513). Then follows, in most cases, either a vertical or horizontal rectangular shape with curved sides, filled with concentric bands of different colours, carved in slight relief. These patterns appear to represent the tattooing on the bodies of the natives, as shown by B. Blackwood (pl. 70, p. 431). The name of "lalom" is given to a lozenge pattern of parallel lines tattooed on the back of the neck of a person of rank. (Schmalenbach, 1956, pl. 15.)

There also exist a number of naturalistic wooden sculptured figures from Buka Island (McCarthy, 1951, p. 182-3). These sculptures bear similar ornaments to those on the paddles on the body and face of one of the human figures, also the same kind of headgear or hair-do, and the extended ears touching the shoulders. This indicates that a body is intended to be represented on that part of the paddle where the geometric ornamentation is placed, but conventionalized sufficiently so as not to lose its meaning to the initiated. It is possible that each of the different patterns belong to a special clan. There is another feature which links the origin of this pecular pattern with a naturalistic prototype; it is the overall trapezoid-like shape which also suggests the elongated body of the kokorra. In most examples an open work of filigree section is added on each side, connecting the pointed corners of the geometric shapes with the shoulders and elongated ears; the latter could be

[8] Blackwood (pl. 70, 1935, p. 431) writes that gom is the term used for cuts on the fact, which usually follow the features to some extent, somewhat like the Maori tattooing, but less elaborate.

interpreted as arms and legs of human body with the typical raised arms, and squatting position of the legs (pls. 4 and 5, B 8921, E 8109, B 8905). It is most clearly seen in E 8109 and in the two examples mentioned above (B 8905 and B 8740) where the full body of the kokorra without ornamentation is carved in open-work showing the pattern formed by arms and legs, connecting the open-work links on the ornamented species of paddles. This feature has been conventionalized in different ways, becoming more and more geometrical and ornamented, and getting farther away from its naturalistic origin (B 8906, B 8742, B 8909 and E 1809, where even feet are indicated by paint). The decoration of the handle with its sculptured head and geometrized body has been developed into a highly artistic unity, thus distinguishing this group of wands from the other groups. In spite of this pecularity this group is connected symbolically and spiritually with the other groups through other motifs which are not particular to this group alone. One of these motifs is a circle filled with a star-like feature, sometimes surrounded by toothed lines in numerous variations (Pls. 4 and 5, B 8906, B 8752 and E 16513.) This circular motif is also to be seen on the breast of the sculptured figures (McCarthy, 1949-52). This motif is used in infinite variety on the discs of clam-shells with a fine piece of turtle shell filigree work superimposed upon it called "pirir",[9] about which Blackwood (1935, pl. 68, p. 422) said: "These highly priced ornaments are worn as pendants, on ceremonial occasions only". The position of this motif on the breast of the sculptured figure, and also consequently on that part of the paddle which represents the body of the kokorra, leaves no doubt that we have here a representation of the same symbol. Blackwood reports (p. 532) that a stone pillar near the village of Iltapan (north-west corner of Buka Island) bears a circular ornament consisting of some concentric circles filled with zig-zags, carved out of the stone in flat relief, and underneath several rows of triangles or zig-zags. The natives explained that the two parts of the pattern belonged together and that in the olden days they used to cut this pattern on their faces.

Group II is a rather uniform group; with few exceptions all specimens follow the same pattern. Relationships between the indicated groups is by a few mutual characteristics. In group I, as well as in group II, the blades are mostly plain, painted white with a red or black point. The motives found on some of the wands are related to some on the paddles in group I: there are the same spirit heads on stands, or the whole kokorra is portrayed in the usual fashion (E 16513), or with a kokorra head and a triangular body filled with zig-zags (B 8921) beside some wing or crab motifs. On the other side of this blade we find a kokorra, and underneath a head of a kokorra with a special feature, almost like a stand, but one which we will see more frequently in group III. The latter motif is a stem growing out of the chin of the kokorra's head ending in two volutes (pl. 5, B 8905).

There are five wands which possess characteristics common to several groups. These are E 8109, B 8758, B 8740, B 8905 and B 721, which I will discuss in detail. E. 8109 has a double-headed sculptured handle, followed by a flat area bearing the geometric ornament characteristic of group II; the whole available space on the blade is covered with decoration, in a different style, as if done by another artist. The usual fully figured kokorra is almost identical on both sides of the blade associated with the chevron, a floral kind of characteristic of group III. The part underneath the sculptured head is of triangle shape filled with zig-zags, whilst the concentric quadrangle pattern is found on the back of the head and a circular motif filled with a floral ornament is carved on the rear side of the body-like shape. The rest of the paddle is filled with a row of chevrons and a well developed kokorra figure. B 8740 and B 8905 (pls. 4 and 5) are exceptions in so far as their double heads belong to the

[9] Reichard (1933, I, p. 107) reports that these ornaments are called Kapkaps and exist over a wide field in the Pacific area where they are commonly worn on the forehead.

two different types, described on page 43, but both have the kokorra body carved in filigree, without the characteristic concentric geometric design of group II, and they both have on the rest of the paddle the type of ornamentation characteristic of group III. B 8740 is decorated with the totemistic symbol of a lizard carved and painted on both sides, followed by chevrons; on one side the kokorra head only, on the other side the whole kokorra is shown. There is a group of wands with animal representations in group III to which I will refer later on. B 8905 is the most interesting and important paddle to my mind in the whole collection and it will be mentioned further on in a different connection. Here it is sufficient to say that it shows the sculptured double-head belonging to the second type of heads (see pl. 5) followed by a kokorra body carved in openwork; the blade is not pointed but flat at the end, showing a remarkable decoration on one side in which, underneath the freely carved body of the kokorra, is a row of chevrons and then a fully featured kokorra pointing towards the end of the blade in the usual way. It corresponds in style exactly with the filigree body in its sensitivity of line, the arms and legs are softly curved and the body is elongated and elegant. The face is different from the sculptured one—the former has a rounded chin, that of the latter is pointed. On the forehead of the former the design is not identical on both sides of the face; it consists of a kind of voluted ornament above which there is the pointed headgear or hair-do decorated with flanges. A ridge runs down from the point of the hair-do, across the forehead and nose down to the chin, giving the whole head a peculiar rhomboid-shaped appearance in contrast to the flat-ended blade. The decoration on both sides of the blade is identical in the chevrons and the kokorra, both being enclosed in a frame-work to form a kind of niche. The freely carved body of the kokorra on the handle is similarly enclosed by a kind of lattice work on both sides of the body up to the sculptured head. So far the decoration of the blade follows the usual pattern of ornamentation characteristic of group III but below the fully bodied kokorra is a unique representation of two kokorra heads posed at a right angle and connected by a band emanating from the chins. The whole design is surrounded by a frame-work characteristic of group III. An ornament similar in its shape to the one on the forehead of the sculptured head is to be seen in the empty corner.

On the other side of the paddle the remaining space on the blade is filled with a kokorra head and the stand-like ornament ending in two volutes. Separated by a neat frame-work, each in its special compartment, we see on the right and left two embryo-like creatures in profile; the one on the left is clearly recognizable as a human being with a large head, with an eye, ending in a pointed chin, and a body with one raised arm, an angled leg and a foot. The being on the other side of the kokorra head is not so easily defined as a human being; the large head ends in a pointed chin-like feature, and the body is in profile, with a kind of arm and a leg. (Pl. 5.) In attempting to understand the meaning of these figures I would suggest that we have here the representation of a whole family; the father is represented by the fully figured kokorra, the mother by the head with the voluted ornament coming out of the head, which might indicate her breasts (see also the unnumbered specimen in pl. 3), and the children are the two small figures on each side of the head.[10] The idea that the kokorra head with the voluted ornament might signify a woman is reinforced by numerous similar representations. There are a number of exceptions in group II, but the wand just described is one of the most extraordinary ones.

B 721, the biggest of this group, about 7½ feet long, is another very interesting exception in so far as it shows the flat white halo, described on page 43, and it is the only example I have seen of this type with a single head (pl. 4). Its large head is tattooed in the way we have seen before on E 16513 (pl. 4) but the body is the filigree

[10] See B 8775, pl. 6, where a child is shown in profile, with the round head in frontal view.

style of B 8905, described above (pl. 5). The blade is plain on one side and decorated with one kokorra head on a peculiar stand on the other side. This is another example which shows that certain types and patterns are always associated; there are also some exceptions which contain features of various types, indicating connecting links between the different types and groups.

There are two more examples which should be mentioned here as they distinctly show features of groups II and III. In shape they belong to group III, being flat and fish-shaped, but their decoration points clearly towards group II. E 26516 shows on the handle the kokorra head followed by the concentric geometric design so characteristic of group II (on both sides); on the side of the blade are the scanty decoration of two heads, one on a stand and the other with the stand-like feature which I compared to a woman's breasts (pl. 6).

The other example is also flat, but in shape similar to those of group II; it is undecorated except for a kokorra head on a stand-like feature flanked by wing or crab motifs on the handle and a stand on the tip of the blade.

Group III. Wands

The wands in this group are not uniform in shape, as there are many variations from the norm, but they all have one feature in common, i.e., the whole available space is decorated. The motifs also vary considerably with a greater variety than in groups I and II. Totem symbols and animals represented realistically include sharks, lizards and birds. The human beings show a greater variety of aspects. Some are seen in profile others are presented full-face. Some of the human figures carry an axe. There is also quite a number of specimens in this group which are decorated with geometric patterns only, or predominantly with a kind of ornament derived from floral motifs.

Group III contains also a great number of unpainted, partly painted and completely painted wands, but I shall not make this a basis of division as the unpainted ones would probably have been painted eventually.

(*a*) *Shape and decoration of group III*

The wands in this group have a number of common features in the shapes of the blades and handle; these combinations are frequent, there are blunt or pointed ends, fish-shaped flat wands, and thicker examples. Some are lenticular in section. It is preferable to arrange the subdivision of group III according to the type of decoration.

They are all more or less flat, some are very thick, especially the lenticular and rhomboid examples. The latter have a median ridge extending from the handle to the end of the blade. (See pl. 6) Some of the paddles are very light, others are heavy and could be used as weapons. The average length of the paddles is approximately 60 inches, but they vary from 44 to 88 inches; the width varies from 4 to 8½ inches.[11]

The motifs are blended in all kinds of combinations, the kokorra, the kokorra head, various kinds of chevrons, diamond-shaped geometric ornaments, teeth or triangular motifs and the circle filled with floral ornaments or geometric patterns. Besides these motives there is a number of exceptional designs and as these are quite

[11] The very small examples seem to be dancing-sticks for women (Nevermann, 1932, p. 200 and p. 225, fig. 144).

frequent I have divided the exceptions into sub-groups according to their decoration, so that we now have the following:—

(a) A combination of various motifs.

(b) Human figures in profile and standing upright.

(c) Kokorra heads continued in coils or scrolls, beside the ordinary heads and kokorra figures.

(d) Animal representations such as fish (sharks), lizards, birds and four-legged animals.

(e) Geometric ornamentation only.

Description of motifs

E 8049 (pl. 6) is typical for this group. It is fish-shaped, slim, 65 inches long and $4\frac{3}{4}$ inches wide, its decoration consists of two kokorras pointing in the same direction towards the handle, a kokorra head pointing in the opposite direction, while the rest of the paddle is covered with chevrons and a wavy ornament. A narrow rim frames the decoration. The design is well executed and the kokorras are carved in an angular rectilinear style, which is concurrent with a more curvilinear design on other paddles. E 7968 (pl. 6) is more elaborate in shape and decoration, partly stained, partly covered with red paint, bearing the fully figured kokorras and also the kokorra head, the chevrons and an interesting kind of frame consisting of different patterns or flanges, zig-zag lines and scrolls or coils. The kokorra on the handle is different to the ones on the blade, which is interesting to note as this variation occurs quite frequently. The remaining space on the paddle is filled with different kinds of chevrons.

Different kinds of kokorras

There are very slim, elongated kokorras (E 7952, pl. 9) and fat ones with rounded contours (E 24669, pl. 9). E 8049 (pl. 6) shows a kokorra in contrast with rather straight lines and pointed contours. Both types form a closed design in contrast to those of an open design (E 7968 or B 8767, pl. 6) where the head is bigger than the body.

Heads

Heads vary in design, too, although they all contain the main features already described. The foremost difference is to be found in the decoration of the forehead. E 24669 (pl. 9) contains three heads, each one with a slightly different design, whilst on the other side of the blade the heads have no forehead indicated at all, a feature which is very seldom seen. The hairline might be a simple line or a zig-zag line, and the hair-do rounded, pointed or onion-shaped, decorated with flanges or with a feather or an ornament on the top. (B 8796 and E 24670.)

Framing

On most examples in group III there is another feature, a framing of the figures, which we have not met in other groups. The edge of the paddle is decorated with a line which follows the contours of the kokorra; it may be a plain, toothed or fringed line (E 8056, pl. 10) or both (E 8057; pl. 6, E 7968). Sometimes the framing takes the shape of an arch or of a complicated fringed and flanged feature as on E 5346, or of an ornamented framework as on E 8079 (pl. 10). This leads to a very

important example (E 8053, pl. 8) which shows quite extraordinary features. This paddle differs from all the others in so far as the kokorra figure is seen in profile, and carries an axe. It is set in what appears to be a landscape, although a kokorra head and body are fused with its details; the framing ornaments on both sides and on top of the kokorra point towards this landscape. If the assumption that this is a landscape is correct, one could also say that the framing in the shape of an arch and similar shapes indicates a building, hut, or an entrance (pl. 7, E 8057) (Lommel, 1956). In view of the fact that this paddle contains a number of naturalistic features, as the kokorras seen from profile and carrying an axe, the idea that the extroardinary framing might indicate a landscape has some probability. We will find in sub-group (b) quite a number of naturalistic representations in the motifs, such as the kokorra seen from the front and those standing upright or in movement. Totem animals, too, are represented realistically. Nevertheless, I am quite aware that the elaborate framing (some of the indentations are pointing upwards and some downwards) may just as well be the playful exuberance of a native with more fantasy and gift for decoration than others who kept more to the accepted routine.

Sub-group (b): human figures in profile and standing upright

These wands display various combinations of the motifs. What they all have in common is that they show, beside the ordinary kokorra, a figure seen either from the profile or standing upright. Some of these in profile are awkward representations, and look as though the artist had forgotten to add the second arm and leg, but the big head is the usual one as seen from the front. (See E 8084, pl. 8, on which one feels that there was not enough space for an ordinary fully figured kokorra as the paddle gets slimmer at that part where the kokorra in profile is to be seen.) Studying other examples of these strange figures, we find that in most cases the outline of the body has changed from a symmetrical to an unsymmetrical body at the point where the line of the side of the body (without the limbs) is nicely curved as on the spirit figure's back. The figure is well placed in the available space. E 7950 is very well designed and executed and shows on one side of the blade three ordinary kokorras and one kokorra in profile. The other side of the paddle also has three kokorras, and on the middle of the blade, on the widest part, a kokorra in profile.[12] E 8037 (pl. 5) has on one side of the blade an ordinary kokorra and on the other side, on the widest part of the blade, a kokorra in profile with a large head, a well curved asymetric body and one raised arm and one leg in the usual way, carved and painted in red and black on a white ground. There is another example (E 8080, pl. 7) which shows only one fat, short-legged spirit with three claws to each foot on one side of the blade, and on the other side a fat asymmetric creature in profile, with an elaborate inside design on the giant head, on an angled neck. This is another naturalistic feature, as necks are hardly indicated. The remaining part of the very slim, spear-like handle is decorated with chevrons only.[13] Then there is E 7981 (pl. 7), a very well-carved paddle which shows various motifs such as the full kokorra on one side preceded by a kokorra in profile and followed by a very elaborately carved circular ornament (filled in the manner of a kapkap) and chevrons, and on the handle a floral or octupus-like motif.[14] The other side of the paddle is decorated with similar motifs and a figure in profile at the point of the blade. B 8775 (pl. 8) also shows a figure in profile at the point of the blade. It is, no doubt, a child with a round head seen from the front without a hair-do. All the wands so far described display a very well-developed framework of different designs. E 8081 (pl. 8) has

[12] There is also one paddle in group I (B 725), which shows on the widest part of the lance-shaped blade a kokorra in profile.
[13] Similar to a paddle-spear, B 8846.
[14] These will be discussed with the geometric patterns.

two ordinary kokorras with chevrons, and a very remarkable creature on one side of the handle; it is a figure in profile but carrying an axe, with the blade upturned, growing out of one of the four fingers of the raised hand. Another special feature of this kokorra is that the ears are elongated and decorated with a triangular-shaped ornament. We can see here a degree of naturalism that we have encountered up to now with animals only, as the human beings were always represented in the same schematized fashion with only slight variations from the same pattern. There are other examples of naturalism associated with conventionalized motifs:—

E 5346 (pl. 8) shows, on the handle, another kokorra in profile carrying an axe on his shoulder and supporting it with his raised hand. His one leg reaches much lower down, as if the little man was sitting (but no indication of any seat) and dangling his leg, another naturalistic feature. The whole body is really seen in profile, and does not appear to be an adaptation or variation of the ordinary kokorra body; it tapers at the neck, but the head is seen from the front. There is that extraordinary wand (E 8053, pl. 8) disscussed on page 48, where a very well designed kokorra is shown sitting on a kind of little hill, his only leg dangling down; his asymmetric body has one arm raised on the opposite side, and an axe grows out of his neck in an awkard fashion, on the same side as the leg, as if the artist did not know how to combine the arm with the axe.

All these strange creatures so far discussed had their heads in frontal view, but E 8059 (pl. 8) shows a kokorra with the body asymmetric and posed from the side, one leg dangling down at an angle, the raised arm supporting an axe with blade upturned on his shoulder. The head in profile has one very large eye, distinct nose and pointed chin surmounted by a very big, ball-shapped hair-do. This is the most naturalistic figure we have encountered so far. The only other similar example is on a paddle belonging to group I, which shows on the lancet-shaped blade a similar little figure, sitting on a stone (?) and carrying an axe on his shoulder.[15] There is also a parallel to this creature in the embryo-like figure looking thoughtfully at his raised fist on B 8905 (pl. 5), described on page 45, where I think a whole family is represented.

We now come to some other examples which are decorated with the usual kokorra in full figure and various ornaments already well known to us, but they also show a kokorra in profile standing upright or in a frontal position. Two of the frontal ones (E 8011 and E 7072) are almost identical in shape and decoration and in the style of design, so that one could think they were carved by the same hand. Both have on each side of the blade one fully figured kokorra in the usual squatting position, very elongated and elegant, followed by chevrons and an ordinary kokorra on one side of the handle; on the other side of the handle, however, is the figure of an upright kokorra, with raised arms and hands touching the ornamented ears and the head in the usual way, but the body ends in two legs standing slightly apart with feet pointing outwards and there is a representation of the sex organs. (See paddle E 7952, pl. 9.)

In the next group there are the upright kokorra with the arms hanging down. These wands are rather similar in shape but quite different in the style of decoration. E 24668 (pl. 10) has one ordinary kokorra on one side of the blade and handle and on the other side is an upright kokorra with the arms hanging down, so as to follow closely the line of the body, with indications of elbows, large hands and the legs parallel with large feet turned outwards. E 8056 (pl. 10) has two standing kokorra on each side of the blade. All are identical and exactly like the above described

[15] Reichard (1933, II, pl. CLI, No. 638a b), a paddle from the Solomon Islands now in Hamburg Museum.

kokorra. E 798, a painted one, has a standing kokorra of the same type on one side of the blade, followed by the ordinary kokorra and chevrons. Besides these more or less typified figures are a few wands with more naturalistic features, especially the one on E 8048 (pl. 12), where the legs are parallel, the shoulders nicely rounded and the arms hanging down casually with hands on hips; the elbows and fingers are well indicated, and a round ornament is to be seen on the chest and a circle (navel?) on the body.

There is another group of wands showing kokorras in various upright positions [E 8052, E 8079 (pl. 10), B 8775, E 7951, E 7949 and B 8759].

E 8052 (pl. 10) is very interesting because it has two kokorra heads side by side above the standing figure, which is represented with hands on hips and legs slightly parted. E 8079 (pl. 10) shows one standing figure on the handle with hands on hips, legs with feet turned inwards and a naturalistic representation of the sex organs. B 8775 (pl. 8) is the small slim specimen (mentioned before) with the representation of a child-like creature in profile. On the other side of the blade is a large standing kokorra, hands with fingers clearly indicated near hips (or on the sides of the body), a feather on the usual big head, legs with knees apart in a kind of hocker position and a representation of the sex organs. E 7955 shows two similar figures, one on each side of the blade, besides two ordinary kokorras on each side. E 7951 (pl. 9) shows a kokorra with large heads arms upraised and the legs in a dancing position. E 7947 (pl. 11) has the shark with a kokorra head on both sides, beside the standing figure of a kokorra, clearly in a dancing position, arms upraised, one leg on the ground, the other slightly raised. There are a circle on the kokorra's chest and a belt near his hips. B 8759 (pl. 9) is remarkable because of the queer kokorra figure on one side of the blade, painted in red and black: it has the ordinary head and body, one arm and one leg raised, the other hand rests on the hip, the second foot on the ground, and what appears to be a seat is indicated by half a chevron.

Pl. 9, E 7995 and E 24669 are the only two specimens which show standing figures in profile. One is decorated with a kokorra with an ordinary head, one raised arm, asymmetrical body, and one leg only in a slightly bent position as E 7949. The other example (E 24669, pl. 9) is a very large one with a broad blade decorated with a squatting kokorra, and one standing in profile with head in frontal view, one arm hanging down with the hand resting on the sex organs, an asymmetrical body and one leg, or both together as seen from the side.

The wands in this group display variations in the representation of the standing kokorra. They possess naturalistic features besides the typical conventional ones, seen on the majority of specimens. Thus there is no development from an annaturalistic to a naturalistic representation, but a parallel occurrence of both trends, often carved on the same specimen. The artists are well aware of the features of living man as well as ghosts and are able to represent them in both ways.

Sub-group (c): wands decorated with kokorra heads continued in coils or scrolls

When we look closely at the kokorra heads, we note as many variations as with the fully figured kokorra. The shape of the face and of the stand on which many of them are mounted is greatly differentiated as with the paddles of group I. There exists also a type of head from the chin of which two coils extend; the voluted endings of these coils might be turned outwards as B 8796 and E 7974 (pl. 6), or turned inwards as on E 8025 and others.

When discussing B 8905 (pl. 5), on page 45, the idea was put forward that this might represent a woman and that the voluted feature might signify

her breasts. This was deduced from the fact that a whole family was represented—father, mother and two children. There is one paddle in group I (no number, pl. 3), which clearly proves that a woman's breasts are intended as a distinct stand is shown below. That there is no neck does not matter, as this kokorra is not a naturalistic representation, but a symbol only. Most of the kokorra heads are sitting directly on the kokorra bodies. The type of kokorra head with the coils is not confined to one group of paddles or wands but is present in all groups. There is one on B 8921 (pl. 5) of group II and another on E 26516 (pl. 6). The latter is a transition from group II to group III, though most examples (E 7998, E 8025 and E 7974) are from group III. Most of the women's heads are confined to the handles (E 8025 or E 8090), but in some cases (E 7974, pl. 6) the whole specimen is decorated with this motif. This one is painted and displays some slight variations of the motif; shoulders are indicated, it has a body ending in two volutes, another head pointing in the opposite direction ending in two coils, followed by a disc, and two more flourishes, as though the artist wanted to add another head but decided against it. The paddle is narrow at this point, so he carved chevrons instead of a head. Variations of this motif are present on the handle of E 8077, whilst the blade shows the ordinary kokorra figure. E 8004 has another variation on the handle: a head with raised arms, as on the painted canoes in the Museum's collection on which the voluted feature underneath might suggest feet. Feet are shown that way on E 8785 (pl. 6), and B 8777 presents another variation of the same theme.

Sub-group (d): animal representations

Birds.—Here we have a group which displays birds beside the fully figured kokorra, the kokorra head and chevrons of all kinds. In discussing the paddles of group I we found that on the leaf-shaped blades the birds were the most frequently used motif. They are represented as seen from above, with heads turned to the side. Some are quite elaborately designed with indications of plumage in different colours, or with the tail feathers only. There is a similar bird on E 8052,[16] decorated with the standing figure of a kokorra below two kokorra heads side by side. The other side of the blade shows two squatting kokorras separated by a bird in the above-described heralding fashion with a rather naturalistic head. E 24670 (pl. 12) shows a bird in profile on the handle associated with predominately geometric ornamentation. E 24668 also has a bird in profile on the handle. B 8768 (pl. 12) shows a realistic bird in profile.

Fish.—The fish are not naturalistically represented, and are difficult to recognize. The figure is a fish-like shape, sometimes with eyes which identify it as an animated being. As the bonito is the most important food fish in the waters of the Buka Passage and its surroundings, I will call this motif the "bonito motif".

E 7966 (pl. 11) is one of the few wands without either a kokorra head or a fully figured kokorra, and it forms a link with the next sub-group, which has geometric motifs only. It has on one side of the blade three fish-like shapes, all with indications of scales; the middle has indications of gills and eyes, joined together without a tail in an ornamental fashion. On the handle the fish-like shape is joined to the chevrons which cover the rest of the paddle so that it looks more naturalistic, as the first chevron forms the tail. On the other side of the handle there is engraved the distinct outline of a fish. E 8100 (pl. 11) has two representations of the bonito-kokorra, namely, the fish body with the kokorra head, associated with different kinds of chevrons, and the other side shows five parallel toothed lines. B 8784 (pl. 13) is a very well carved example on which both sides bear identical motifs, i.e., a bonito

[16] E 8057 shows a similar bird between ordinary kokorra and kokorra heads, and on the other side a bird without a head. See also E 7985, pl. 13.

motif on the butt, surrounded by long thin denticals (as on E 8100), and on the handle a bonito combined with another motif, probably a derivation of the kokorra arms and legs. In a shield from south-east New Guinea similar motifs are to be seen. E 24668 (pl. 10) has a bonito-kokorra on the handle beside what appears to be a bird. E 8001 (pl. 5) has a naturalistically represented fish amidst the kokorra figures.

Shark and shark kokorra.—In the same way as we saw representations of naturalistic fish, and also fish with kokorra heads, there are many realistically represented sharks with all their characteristics, and there are also sharks with a kokorra head. E 8062 (pl. 11) has on the blade a very well carved shark as seen from above, in the right proportions, and a similar shark is to be seen on the handle of E 8077 with the fins painted black and the body red. E 7947 is a very interesting wand with a dancing male figure and a shark-kokorra on both sides of the blade, (pl. 11). The kokorra head is well integrated with the shark's body and the ears of the kokorra do not point downwards but are horizontal and fin-like, and the hair-do is ornamented with a pattern of concentric lines. The shark-kokorra on the other side of the blade is fitted with two pairs of horizontal ears and the chin line is accentuated with two rows of zig-zags, which could be either a necklet or indicate the gills of the shark. There is a very slim shark-kokorra on one side of E 8066; the rest of the space is filled with chevrons and zig-zags and one kokorra head. A shark-kokorra painted in red and black is to be seen on each side of E 8108 which shows a blunt angular butt, whilst most examples in group III are fish-shaped, flat, slim and without a specific handle. E 8050, painted in black and red on a white ground, shows another version of the shark-kokorra: the slim body of the shark ends up in two arm-like features which surround the kokorra head. E 9780 and B 17055 show the same shark-kokorra as E 8108 on both sides of the blade, and E 8066 has the shark-kokorra on one side only. B 8749 (pl. 12) is exceptional in having the shark-kokorra on one side of the blade and on the other a fully figured squatting kokorra, but this time (and this is the only example) the arms hang down[17] underneath a kokorra body without head or legs, also with its arms hanging down on both sides of its body. On the other side of the handle is the bonito motif with big eyes and a body without a head, but with raised arms and legs.

Lizards.—Only four wands are decorated with lizards. Three of these are naturalistic representations and one is a lizard-kokorra. The most realistically represented lizard is on E 8061, as seen from above, with a tail, angular legs and a head with two large eyes (pl. 11). Above the lizard is a kokorra head with two coils coming out of the chin. One black lizard is carved on each side of the blade of B 8740 (pl. 4), belonging to group II, in the same naturalistic way as on E 8061. This specimen is an exception in group II in so far as it has the fully figured kokorra on the handle carved in filigree, and the blade is fully decorated. E 8067 shows a similar lizard on one side of the blade, but with its head turned sideways, and E 8063 (pl. 11) shows the lizard with the kokorra head, the raised front legs with four fingers resembling the raised arms of the fully figured squatting kokorra.

Four-legged animals represented in profile.—There remain only two more wands to be discussed, B 738 (pl. 3), belonging to group I, with four animals in profile standing opposite each other; a pair painted in opposite colours are standing on one side of a ridge which runs along the middle of the lancet-shaped blade, facing a similar pair. It is difficult to identify these animals, they might be pigs, dogs or possums. One pair has raised tails and no ears, the other pair has tails ending in a scroll and big ears, and all of them have only one large eye. There is also one wand in the Tasmanian Museum, belonging to group III, which bears one of these animals in profile (as on B 738) with a raised curled tail and one large ear.

[17] Paddle E 7928 from group I shows on the blade a fully figured kokorra with one arm raised and one arm hanging down.

Sub-group (e): geometric ornamentation

There are many wands in this sub-group, and most of them belong to group III according to their shape. Many of them show one or two kokorra heads between the ornaments (E 8808 and B 8796, pl. 6, with woman-kokorra); others have one side decorated with ornaments only, and on the other side the kokorra head. Some are decorated with geometric decoration only. (E 7965, B 8788 and others.)

The main motif is the chevron in a variety of shapes and forms; other motifs are the circle filled with a variety of minor motifs, some clearly showing their origin in the plant world of the islands; other ornaments are the toothed lines, or denticals, flanges, zig-zags, scrolls, dots and the wing or feather or crab ornaments. We will deal lastly with the complicated and involved patterns of high artistic standards often derived from the zig-zag.

Chevrons (see fig. 1).—This most commonly used ornament varies from very large and simple ones which cover the whole wands (E 8764) to very small ones. The large chevrons measure up to 6 inches in length and 4 inches in width and the small ones up to 2 inches x ½ inches. The sides of the chevrons are either curved or almost straight. Some show a very slim stem, as on B 8896 (pl. 13) and E 7981 (pl. 7); others, like E 8080 (pl. 7), show different types of chevrons combined, as also on B 8896. A common type of chevron, as on B 8784 (pl. 13), is combined with the bonito motif and forms the tail of the fish; others are reminiscent of the eagle or other birds. Some chevrons are combined to form new patterns, as on E 8061 (pl. 11) and E 8073, and, foremost, on E 24670 (pl. 12). Chevrons might form irregular-shaped lozenges, as on B 8783. Quite different types of chevrons might appear on one paddle in connection with representational motifs. E 7985 (pl. 13) shows a combination of chevrons and floral motifs, which link them with the next motif, the circle.

Circle.—The circle is never perfectly shaped, but is mostly crudely executed and of irregular shape. We saw it on the bodies of kokorras on all groups, and in combination with the birds in group I. The circles might be filled with geometric designs, or designs derived from the petals of flowers or marine life.

B 8788, a nicely carved and painted wand, shows the chevron motif combined with four filled circles on both sides of the blade. These are not perfectly round circles but are rather odd-shaped ones filled with six and seven petal-like flanges respectively. B 8914 (pl. 14) has one plain unfinished side, and is a very crudely shaped unfinished wand; on the other side are five flower motifs in an oval of very large size. The biggest flower is 11 inches in diameter, and is reminiscent of a poinsettia in the irregular shape of the petals.[18] This motif is also present in a simplified form on E 8057 and E 7985. B 8788, a nicely carved and painted paddle, has the chevron motif combined with four filled irregular circles on one side and three on the other side. The last-mentioned flowers have from 13 to 15 petals in alternating bichromes of red and black, or monochromes of red or black only.

The circles filled with geometric ornaments vary from the most primitive to much refined ones. This motif occurred in group II (pl. 4), on the carved bodies of kokorras, where its resemblance to the more complicated and refined patterns of the pirri or kapkaps was observed. (See B. Blackwood, pl. 68.) On the pirris the patterns of basic elements are much more intricate and varied, perhaps because of the harder material in which they are executed. B. 8794 shows a very simple filling, consisting of a cross with curved arms, E 8065 has a more complicated star-like

[18] This wand is different in style from all the other wands and does not seem to come from the same district as the others, as it says on its label New Britain (?). The poinsettia has been introduced by the white man to the islands and is doing very well there.

composition in the centre and E 7981 (pl. 7) had a toothed-line added to the circle (fig. 1). The latter wand bears also a circle filled with a flower motif or octopus motif, on which there are 10 arms in a whirled design. The circle filled with ornaments and surrounded by the toothed-line leads us to another very important element in the decoration, namely the very frequently occurring triangular patterns, toothed-lines and denticals. These patterns are used a great deal and in widely different sizes. Small denticals are used to decorate the bodies of the bonito motifs to indicate scales (B 8784, pl. 13), others are used to indicate feathers on the bodies of birds (E 1159 of group I, pl. 3), some are meant to suggest gills of sharks, others again illustrate necklets (of sharks' or dogs' teeth) on kokorras (E 16513 of pl. 4). Some of the triangular ornaments are used for decorative purposes only, such as framing of kokorras (E 8056) or as a single motif by itself. Some of the triangles are up to 4 inches long (E 8100, and one with no number, pl. 13). Some are flange-like and decorate the hair-do of kokorras. (E 16513, pl. 4, E 8905, pl. 5.) Circular ornaments with fillings of triangular shapes or tooth-lines are also to be found carved on the surface of a stone pillar at Yltopan in north-east Bougainville. (B. Blackwood, p. 77).[19] Underneath the circle is a pattern consisting of rows of triangles, one of the most frequently occurring patterns of this type on the pillars and on the paddles and wands. (E 8052 and E 7965, pl. 10.) We then have a wand (without a number, pl. 13), decorated with geometrical ornaments only, displaying a sample of most of the geometrical designs, such as triangles, toothed-lines, denticals, filled circles, large chevrons, all painted red and black on a white ground. The way it is ornamented, leaving very little empty space, leads to another example (B 8896, pl. 13), which is very interesting in several ways. Its overall shape resembles a paddle-spear, with the blade of a paddle, and, instead of a handle, the pointed carved ending of a spear. The type of ornamentation on the handle is different from all the paddles we have seen so far, being crowded with ornaments of an entirely different style alien to the district of Buka Passage.

Zig-Zags and various other geometric ornaments.—The five specimens to be discussed possess various geometric motifs which are quite unique and of high artistic standard. Two of these wands are very similar in shape, rather unformed, without a specific handle, narrowing at the end; B 8809 has on one side a kokorra head amidst two different types of chevrons, and on the other side an unusual zig-zag pattern almost identical to that on B 8786 (pl. 14). The pattern consists of a ribbon, three-quarters of an inch wide, which runs in a zig-zag along the whole length of the paddle, and has a flattened side where it turns. This device gives a strong emphasis on movement, especially as the ribbon is painted in alternating red and black colours on a white ground. This pattern is usually found on a board called watsinan, which is part of a boat (mon) (B. Blackwood, page 435). The name of this key pattern is dore. The so-called watsinan is a plank on the bow of the plank canoe. This pattern is quite unusual on the wands and it is possible that the unfinished B 8786 was originally carved as a watsinan and later on changed into a wand. It is quite flat in profile, similar to B 8914 (pl. 14) with the poinsettia decoration, which is also unfinished, unshaped, flat, and in a way differs from other paddles.

E 7971 is also unusual because the pattern is expressed by the nagative parts in a white star-pattern formed by the ground, after some elaborate shapes had been carved in the usual low relief and painted red and black (pl. 14). The two sides of the wand are identical in their reversed colours. This is a sophisticated, accomplished

[19] Blackwood, 1935, p. 539. The exact origin, age or meaning of this and other stone pillars are not known. Stone pillars seem to have had some phallic importance and played a part at fertility rites.

pattern, as the one on B 8766 which shows quite complicated lozenges with curved sides following each other along the whole length of the paddle, forming a lively and interesting pattern on both sides of the blade (pl. 14). B 8768, mentioned before, is a very well carved paddle showing interesting patterns on both sides of the blade, among which it has a bird, a water-fowl, totem symbol of the Nakarib clan of Buka in profile carved amidst geometric decoration; the pattern is formed by triangles, which cover the point of the blade, the circle filled with petals on one side and a circle filled with a star-like cross which is used to decorate a fish-like shape, on the other side. The geometric pattern is formed by a kind of rounded chevron, reminiscent of the heraldic bird motif without a head. These chevrons are carved sideways, confronting a middle part with which they form a complicated pattern (pl. 12). Ordinary chevrons fill the empty spaces on both sides of the blade.

There remain a number of minor features to be mentioned, such as dots or small discs, used independently as ornaments, as on E 8057, then a chessboard pattern B 8749 (pl. 12), some patterns formed by concentric lines on E 8087, different kinds of patterns used for the framing of representational motifs, which vary considerably. All these are used freely, but I could not establish any rule or connection between them and the main features. Some masks from Bougainville show a similar combination of patterns scrolls, coils, discs, triangles in rows, mentioned by R. Parkinson (fig. 124, p. 658).

2. THE DISTRIBUTION OF PADDLES IN THE PACIFIC AREA

The paddles of group I are used for transportation and not for ceremonial purposes, and their shapes are accordingly the simplest and the most functional at the same time. They are used whenever the paddler is seated to do the rowing in contrast to the natives who are standing upright as in some parts of New Guinea. The lancet-shaped blade is, however, very widely distributed amongst the natives of the Pacific Area. In Papua and New Guinea the type of paddles used for transportation are different from the ones from Buka; they are short, shovel-like blade paddles. Some show a heart-shaped blade, which also exists in the Eastern Solomon Islands, but have nothing in common with the ceremonial wands from Buka. They are not decorated as a rule, but Haddon and Hornell represent a small paddle from New Guinea with an almost lancet-shaped blade decorated with a short median ridge running down from the tip of the blade and ending in a stylised serpent resembling some paddles from the Cook Island. (Haddon and Hornell, 1936-8, p. 309, fig. 176.) T. Bodrogi (1961, fig. 7) illustrates some paddles with carved decoration on the lancet-shaped blade. The paddles used for transportation in the islands belonging to the New Ireland group are in shape exactly the same as the ones in group I from Buka. They are lancet-shaped and pointed, some showing slight shoulders. They sometimes have different patterns on each side of the blade in the same way as the Buka paddles and the colours are the same, namely, white for the ground and red and black for the carved patterns; sometimes blue is added, but there is no blue in Buka. The patterns are different from the Buka designs, but there is a close stylistic resemblance in so far as the ground is included in forming the design, the combination of geometric and zoomorphic motifs such as lizards, fish, and birds are similar, and the accentuation of the short median ridge is remarkable. Although there exist dancing-clubs and spears on the islands, the only dancing wands appear to be those used in the Trobriand Islands of an entirely different shape (Stephens and Graebner, 1907, pl. VI). From New Britain, R. Greiner, in her description of the Polynesian designs, reports the existence of ceremonial wands decorated with triangles, crescents, fish and human forms, but I have not seen any illustrations of them.

The lancet-shaped paddles, however, are used as far west as the island of Aua in the Ninigo group, situated north of New Guinea. Parkinson, (pl. 29, p. 448) reproduces a photograph of a village scene from that island, where the natives are seen carrying paddles in their hands, exactly the same shape as the ones of group I from the Buka district. It seems, however, from that photograph that the handle of the paddles is longer than on the Buka paddles, and the lancet-shaped blade is smaller and shorter in relation to the overall length, as on the Buka paddles.

Guppy (fig. 1, p. 63) illustrates a photograph of a model canoe with paddles made by a St Christoval native, which shows the lancet-shaped blade and the long handle to which a crutch is added, whilst the blade is slimmer and blending without transition from the handle into the blade. It also has a ridge running along the blade, but is otherwise without decoration. Guppy also speaks of clubs, which he saw the natives of Florida carrying, with "flattened oval blades like that of a paddle". From the illustration he gives of the head of this "Florida-club", it looks to be very similar to some paddles in group III in the Buka district.

Bernatzik (1935, p. 65, III 124) shows paddles from Owa Rahu (Eastern Solomon) very roughly finished, with a crutch with a shorter handle and wider blade, rather nearer in shape to the paddles of group II, which were described as paddle-clubs or wands. Nevermann (1952, p. 127) illustrates three paddles from Emir Island, St Mathias Group, which correspond in size and shape to those of group I, but not in the decoration, which here is purely geometric and utterly different in style, although they are carved and painted in the same way as the ones from Buka and some of the elements of the patterns might be found all over the Pacific area. There is one paddle in the collection of the Australian Museum, B. 8896 (pl. 13), which is in shape and decoration nearer to group III than to group I, with a very long and spear-like handle, ending in a point with a kind of knob towards the end, which corresponds in shape very closely with those from Emir Island (Nevermann, 1932, III, 126). The decoration of the blade shows one kokorra on each side of the blade, besides very well shaped and carved chevrons which become smaller towards the end. The last third of the spear-like handle is carved all round with chevrons on both sides and a triangle pattern in between. From the knob onwards, only triangles form the decoration. From a photograph by Nevermann (1932, pl. 15) one can see clearly that the natives from Tench Island also use the same type of paddles. On the Admiralty Islands a paddle very similar to one from Buka Island, group I, is used; although it does not have the same elegance in shape and outline, it possesses the same proportions of handle and blade. The blade of the paddles from the Admiralty Islands are mostly plain like those in the Buka paddles. Some have a decoration of geometric patterns, carved and painted, representing, according to Nevermann (1932, III. 183, p. 287) stylized birds. Birds in a heraldic shape are the main decoration of Buka paddles beside the kokorra motif.

In the Carolines, further to the north of the Admiralty Islands, very similar types of paddles are in use for transportation. On most of them, the blade blends without marked transition into the handle, which is cylindrical in shape. The cross-section of the blade is similar to those of Buka Island. Some of the paddles from Tobi and Songosa in the West Carolines have a shorter and wider blade, but some are just as slim and lancet-shaped as the ones from Buka and the West Solomon Islands. On the island of Palau and Yap there are several types of paddles to be found. From Yap Mueller-Wismar (1932, p. 177, figs. 259-60) illustrates one which is used for steering and is in shape similar to the paddles in Buka group III. It has a cylindrical handle, distinct shoulders where the blade begins and the blade has parallel sides ending in a point.

On Palau (central Carolines) the paddles are a variation of the same shape with a slight variation in the shape of the blade and the way it arises from the handle. some have distinctive shoulders and a diamond-shaped cross-section, others have a wider or slimmer blade, some are decorated and some are not. Some have a little knob at the point of the blade which produces a singing noise when pulled through the water. (Kraemer, 1932, p. 318, fig. 211, p. 182, fig. 164.) Most of the paddles used for transportation are plain or painted red. The decorated paddles are used for dancing, and a photograph by Kraemer (1932, p. 274, Taf. 16) shows this quite clearly; the women are seen standing on the platform of their dancing house, holding the paddles with their right hand with the decorated blade towards the onlooker and the other hand resting on the shoulder of the next dancer.

On Palau, a special kind of double paddle is used for moving the rafts, and the same type is used as a dancing-paddle decorated on the handle with geometric designs. On Mogemog Island (central Carolines) a paddle is found very similar to the Buka paddles in shape and dimensions but not as elegant and pointed. It also has pronounced shoulders where the blade starts, similar to the ones from Mokil, Nukuoro and Kapingamaranga (Ponape group) (fig. 2, 16-28). The paddles from Pingelap, another island of this group (Eilers, 1932, p. 430, fig. 280-3) are of the same kind as the above described, but are decorated with simple geometric patterns, carved and painted in black and red, sometimes in different patterns on each side of the blade. The handles are painted black, some of the patterns are in red, and the yellow ground of the natural wood may be regarded as a third colour.

On Ponape Island, two types of paddles for transportation are mentioned by Hambruch-Eilers (1932, p. 318, figs. 122-3). One has a slim lancet-shaped blade with a knob at the point, as on the paddles from Palau, a cylindrical handle and slight shoulders. The overall length is 168 cm, length of blade 65 cm, width 10.6 cm; the material is the wood of the bread-fruit tree. The other type is much shorter and shows a different type of blade—wider, shorter with distinct shoulders, an overall length of about 90 cm, length of blade 45 cm, width 12 cm. This paddle might have been used for steering. Some of these paddles are painted red.

For performing the paddle-dances a longer paddle, similar in shape to the one described above for steering, is used richly decorated and painted black. Hambruch-Eilers (1932, p. 204, figs. 13-24) show in their illustration fourteen different paddles varying slightly in dimensions, all decorated with different geometric patterns, which will be discussed later.

The same type of lancet-shaped paddles are also to be found on Kusae (east Carolines) and on the island of Rongerik in the Marshall group (p. 229, fig. 124). The paddles from Kusae are painted black and the ones from Rongerik are wider than the ones from Kusae.

On Nauru Island a very simple paddle is used for transportation; its cylindrical handle merges into a lancet-shaped blade, which is slightly rounded on one side in cross-section.

In the Cook Island group a number of differently shaped paddles are used; the original lancet-shaped blade was changed under European influence according to Buck (1944, p. 179, pls. 190, ff.). He described the old type of paddles as being "shouldered blades with greatest width nearer the tip than the shoulders and with a raised median ridge extending for a varying distance from the tip on the front of the blade". (a and c.) About the carved and painted paddles, (p. 198) he writes: "In paddles for some social functions the craftsman did away with the blade shoulders and omitted the medial strengthening ridges of the tip". These paddles are made of

light wood and it seems clear to me that these are dancing-paddles. (d) Although the paddles of the Cook Islands are short-bladed they are interesting in view of the variety of shapes and their decoration. There also exist in these islands clubs of different shapes which are related to some of the wands of Buka group III, such as the very slim fish-shaped ones, illustrated (p. 27, fig. 172 e and f, by Buck). Also some wide-bladed clubs, especially from Rarotonga, whose shape is the same as one of the blades in Buka group II. The clubs from Mangali have some similarity with the shapes of Buka group III.

Guppy (1895, p. 74, fig. 6) illustrates a "Dance-club of Treasury" which is exactly like some of the paddles from Buka group II. Guppy also speaks of a "flat bladed St Christoval club" which he thinks had its origin in paddles that came to be employed also for the purpose of defence, and their form and material were changed until their original use was either lost or forgotten. He mentions further an ornamented club, which was carried at dances at Bougainville Straits village (east of Bougainville Island) and of an almost identical one he saw in the British Museum from New Ireland.

This mention of "dance-clubs" and their similarity to the "ceremonial paddles" brings us to a number of paddles from Buka, which are very slim and much shorter than the usual ones used for ceremonial purposes. They might have had their origin in either the clubs used for ceremonial purposes, or are derivations from dancing-sticks, which are often seen in the islands and used by women at dances. These dancing-sticks are always ornamented and their motifs are related to the ones seen on spears, which are also used at ceremonies. From this evidence it seems safe to say that all these implements, including clubs, paddles, spears, dancing-sticks and ceremonial axes, which are made from a light wood and elaborately decorated, are related to each other and that they are the ceremonial shapes of real weapons, meant to symbolize the kind of dances at which they are used. R. Parkinson (p. 304, pl. 20) illustrates dancing-sticks from St Mathias, and Nevermann (1932, p. 358, fig. 206) also mentions a "dancing-sword" for women from the Admiralty Islands.

The Buka ceremonial wands (E 7959, E 8042, and E 7990 in pl. 13) in the collection of the Australian Museum which resemble dancing-sticks are exactly small replicas of wands in group III, mostly decorated with geometric ornaments, but an occasional kokorra is also represented. The geometric patterns are usually chevrons and ornaments clearly derived from plant motifs. Their dimensions vary between a length of 41 to 51 inches and a width of $3\frac{1}{2}$ to $4\frac{1}{2}$ inches, this being approximately half the size of the majority of the other ceremonial paddles in group III.

On the Hawaiian Islands the short wide-bladed paddles are used for transportation and no ornamented dance or ceremonial paddles are recorded from these islands.

In New Zealand, however, the paddles used for transportation have the same shape and proportions as the paddles in Buka group I but they are shorter, between 4 and 5.5 feet, whilst the ones from Buka are mostly from 6 to 7 feet long. The side view is different; according to Haddon and Hornell (1926-8, fig. 145b) it shows a paddle with the same stand-like ornament as on some of the paddles in Buka group I. There is also a type of truncated paddle used by the ancient inhabitants of New Zealand, the Moriori, which resembles in shape some of the paddles from Buka group III, only the latter are much more elaborately shaped and show a much greater variety of forms.

On p. 212, Haddon and Hornell illustrate an interesting carved ceremonial paddle from the Bay of Islands. In has the lancet-shaped blade fully decorated with carved geometric ornamentation in the rich style of the Maori and in between there seems to be the representation of two tikis. The handle branches into two

arms united in a plain cylindrical straight shaft ending in a knob. There is also a very beautiful lancet-shaped paddle, decorated with geometric spiral ornaments, reproduced by Lommel (1962, p. 18, Abb. 15). Haddon and Hornell (1936-8) illustrate further "an oar-shaped implement, 7 feet long, which may have been used as a steering paddle, but probably functioned as a club". Here again we have the fusion of clubs and paddles, mentioned before, that have some resemblance to the Buka ceremonial wands, which have approximately the same length and shape of blade, but are more elaborately shaped in the handle and always are richly decorated. The paddles from Buka group II appear to have their origin in clubs, and there is a club from the East Solomon Islands in the Australian Museum collection which has exactly the shape of the blades of wands (E 36513 and B 721, pl. 4) from Buka group II.

As a conclusion of the survey on paddles and wands on the islands surrounding the Solomon group one could say that there are mostly three types of paddles used for transportation: (1) the paddles with a lancet-shaped blade corresponding to the paddles in Buka group I; (2) those with a short and wide blade, which have no connection with the paddles from the Buka district; and (3) the elongated truncated paddles, sometimes used for steering, which have some affinity to paddles from Buka group III.

Decorated dancing or ceremonial paddles are used in the Caroline, Cook and other islands which are derived from the working paddles, but nowhere else is such a wealth of shapes and forms to be seen as in the western part of the Solomons.

3. DISTRIBUTION OF DECORATIVE MOTIFS

(a) Kokorra

After surveying the different island groups surrounding the Solomons, one can state that nowhere, except on a more reduced scale, could we find a combination of anthropomorphic, zoomorphic and geometric designs as decoration of ceremonial paddles as is the rule in Buka. Here the kokorra is the prevailing anthropomorphic motif which occurs in different shapes and forms, mostly accompanied by a wealth of curvilinear and rectilinear ornaments. The greatest variety in the representation of the kokorra occurs in group III. The kokorra is the ancestral being or spirit of the dead represented in a posture of adoration, with arms raised, legs in a squatting position, with giant head and onion-shaped hair-do, big eyes, wide nose and elongated ears. The body is more or less thinly shaped with wide shoulders and hips, the outlines of arms and legs delicately drawn, sometimes showing fingers or toes, but mostly block-shaped, pointing inside or outside. This is the basic motif of which variations range from figures seen from the front, standing upright, or in profile with arms hanging down the sides of the body and feet in different positions. These figures are usually shown in a static position; only very rarely do they suggest movement or animation (B 8759, pl. 9).

In the following chapter I will try to follow the motif of the kokorra in its various shapes in the surrounding areas of the Pacific. A very interesting review by Lommel (1962) is of great help in this regard, as therein is traced the occurrence of the ancestral beings in different cultures and areas. The author traces the squatting figure in the widest sense of its symbolism, including the prehistoric forms as a presentation of the primaeval mother, as a symbol of fertility and reincarnation, as an evil spirit and as an ancestral being. Here we are mostly concerned with the motif in connection with the ancestral figure in the posture of adoration and its variations. These we find distributed in a wide area from Indonesia and New Guinea to the Pacific Islands. (A. Lommel, 1962, p. 35, map 3.) Lommel mentions the

earliest representation in a linear style as far back as the 3rd and 2nd milleniums B.C. on Chinese pottery in the characteristic shape of the letter W on top of the letter M. We also find the same figure in more recent times in rock-paintings from north-west Australia (A. Lommel, 1962, fig. 57), on a bark scratching from the Chatham Islands (east of New Zealand) in Lommel, fig. 37, and on a painting on wood from the Banks Islands, fig. 40, where other motifs, as the circle surrounded by triangles appear too in the same way as we find them on Buka paddles. Schuster (Genealogical patterns in the Old and New Worlds, fig. 1) represents a club from New Ireland with squatting figures and big heads, the body filled with chevrons, transformed into a geometric pattern.

Further to the west we find the squatting figure with raised arms on woven material from Borneo, joined together in rows, sometimes easily recognizable, sometimes very conventionalized to form geometric designs. The same motif is to be found in the Solomon Islands on carved pieces of Tridacna shell plaques, used on the gables of skull-houses. (Bodrogi, 1959, fig. 151; Wingert, 1953; Lommel, 1962, fig. 98.) Similar figures appear in the Marquesas (Greiner, 1923, pl. XVIIg) carved on wooden bowls from Bukava village and on hairpins from the Papuan Gulf and the Sepik River (Reichard, 1933, pl. CXXXVII).

One of the variations of the kokorra motif, a double kokorra, finds its exact parallel in an incised drawing from the Pi-wan tribe in Formosa (Taiwan). (Chen Chi-Lu, 1961, fig. C, pl. 124) and on paintings from north New Guinea. In both cases mentioned, we see one body carrying a head on each side and two pairs of arms or legs.[20] (E 8001, pl. 5.) There is a very close affinity between the carved and incised figures from Taiwan and Hainan Island, and also from the Philippines, with the representations from the Pacific area, as pointed out in a paper by Chen Chi-Lu in the above mentioned Bulletin. The affinities between these islands and the mainland of China is also very close and examples from very early times (Shang, 2000 B.C.) also exist which show the same motif, the human figure, either squatting or standing upright, with raised arms. (Chen Chi-Lu, 1961, pl. 115, figs. M-O.) (The closest parallel with the kokorra head is after all the Chinese Tao-Tieh.)

From this evidence one can see that the kokorra figure is one of the most important motifs in the Pacific, and also on the Chinese mainland, although the kokorra does not appear as frequently on the ceremonial or dancing implements of other island groups as on the Buka ceremonial paddles. In another artistic medium, that of sculpture in the round, the motif is much more often used, whilst the dancing implements of the different island groups mostly use geometric patterns as decoration.

There are more parallels to be found between the upright kokorras (as seen on E 8011, E 8048, E 24668 and E 8056 etc., pls. 10-12) and the fully sculptured figures from the Solomons than in the field of decoration. Sculptured standing kokorras are found on spears from the Admiralties, on Hainan Island and on Formosa. The human figure also plays a dominant part in the overall decoration of New Guinea, where it commonly appears highly conventionalized on shields and memorial tablets, carved in flat relief and painted. (See Bodrogi, 1961, pls. IV-V.) The human figure is represented with raised arms, standing upright, legs slightly apart.[21] We find it with arms hanging down, the same accentuation of the elbows and knees, feet in block-shape turned outwards, and the sex organs represented identically (as on E 8079 and others, pl. 10), painted on a memorial tablet from the Gulf of Papua

[20] Even the design on the face, the way the nose and eyebrows are given, is the same on the kokorra heads from the Solomons and the heads from Pi-wan.

[21] Mr F. D. McCarthy tells me that there are similar figures to be found on petroglyphs from Hawaii (J. F. E. Stokes, 1910).

(Wingert, 1953, p. 100). Another example of an upright kokorra is to be seen carved on a Samoan club (Greiner, 1923, pl. XXV, b) as a standing figure, carrying a two-pronged spear and a club in its hands. There is also a standing figure represented on a wooden board from a house in north New Ireland, with giant head, big ears, arms raised to hold on to two side panels decorated with carved and painted lunar and solar symbols, similar in character to the design of kapkaps from the Solomon Islands. (Bodrogi, 1959, fig. 95.)

In this connection a sarong from East-Sumba (Indonesia) should be mentioned; it bears a Kauri application of a human figure exactly in the same position as the kokorras on E 7962, E 7952, B 8775 and E 8011 (pl. 9), namely, with raised arms, legs slightly apart, an accentuation of the knees and the same sex representation. The feet with five toes are turned outwards and between the legs is a lizard in Kauri application, and a fish on each side of the human figure as well. Small circles and star-like ornaments fill the surrounding ground of the cloth. (Basel Mus., 1961, pl. 19a.) See fig. 2, 1-8.

Kokorra motif as seen from the side or in profile

Very few parallels could be found for the representations of the kokorra in profile. As with most of the anthropomorphic and zoomorphic representations in the decoration of the Buka paddles, some are present in the art of the New Guinea tribes. A. Lommel (1962, p. 50, fig. 43) shows a squatting figure, arms resting on the knees and chin on hands, in profile in a two-dimensional decoration from the Asmat district, west New Guinea. From the same district, Lommel (1962, p. 51, figs. 44) illustrates a shield decorated in slight relief with an abstraction of this motif. He further illustrates (1962, p. 78, fig. 76) another shield from the North-West River, New Guinea, with a similar representation, corresponding with the motifs of kokorras in profile on the paddles from Buka (E 8001, E 7950, pls. 5 and 7, and E 8075, E 8037 and E 7995). T. Bodrogi (1959, fig. 109) also illustrates a dance-shield decorated with a similar conventionalized figure in profile as shown by Lommel (1962, fig. 44) from Witu Island (Bismarck Archipelago). Another example of a figure represented in profile is illustrated by Lommel (1962, p. 53, fig. 46) from an Hawaiian petroglyph, in Honolulu. (Stokes, 1910, p. 33, fig. 1.) See fig. 2, 9-11.

Kokorra—heads

The head of the kokorra is not as frequently used as decoration on the Buka ceremonial paddles as is the fully bodied kokorra. Mostly the head is coupled with a stand for which I have no explanation. There are many variations of the kind of stand used, such as the ones I described on pages 40-41 as being the symbols of a woman's breasts, and there are others which appear combined with the kokorra-head in the shape of scrolls or animals' bodies, or simply geometric ornaments. Boas (1955, p. 23, fig. 10) illustrates a paddle from New Ireland with a kokorra-head on a "stand", but I think it comes from Buka as it is identical with quite a number of paddles from Buka and distinctly different from the paddles from New Ireland. Paddles decorated with demon faces are used in New Ireland.

There are many similarities in the shapes and designs of faces from New Guinea and the Buka district. According to T. Bodrogi (1961, p. 155), elongated ears and earrings are almost an integral part of the picture, teeth marked by carving of triangles are the same in both districts, as are the colours (white ground, red and black designs in slight relief), and there are no difference of details in the portrayal of men and women—spirit faces occur more frequently in New Guinea, on a number of objects, whilst in the Buka district they are most likely to be found on the ceremonial

paddles and on boats. According to T. Bodrogie (p. 75), there exist "bull-roarers in Melanesia which symbolize the dema, the totem of the clan, the spirit of the dead, the personal ancestor". These are used at ceremonies, are named after dead persons and are often hidden from the sight of women. Figure 34 shows a bull-roarer from the Yabim district decorated with a demon's head with a kind of head-dress and underneath the head a pair of arms with hands and fingers similar to the decoration on B 8796 and on canoes. A spirit's head with a head-dress is carved on wooden bowls from the Tami Islands (G. Reichard, 1933, pl. XIV). Firth (1936, p. 75) illustrates ceremonial objects of the type known as Kwoi from the Baroi River and from Maipua (Papua). They are carved and painted in dark red, black and white, one is decorated with a head only, whilst the other one shows a head on top of a kind of lizard.[22]

There is another Kwoi illustrated on p. 76 showing a highly conventionalized human face from Maipua, and, from the Gulf of Papua on a wooden shield, illustrated by Bodrogi (1959, fig. 13, p. 70, 76), a spirits' head surrounded by geometric ornament.

P. S. Wingert (1953) illustrates three carved blades of "Long Staffs" from New Zealand, which show spirits' or ancestors' heads followed by carved curvillinear geometric ornaments. R. Greiner (1923) mentions that spirit heads appear in the decoration of cult objects from the Marquesas and the New Britain islands. Thus highly conventionalized spirit figures and faces are found on the art of almost all of the island groups in the Pacific, but mostly in New Guinea. They are carved in slight relief on different objects, as on bull-roarers from the Yabin, and on ceremonial shields which remind me strongly of the Tao' Tieh' masks on the Chinese cult vessels so frequently seen on Shang bronzes.

Sculptured double (Janus) heads

The fully sculptured double or single heads, as they appear on the handles of the paddles from group II only (pls. 4 and 5), also find their parallels in New Guinea, as do most of the motifs from the Buka paddles. According to T. Bodrogi (1961, p. 177), Janus images and double figures frequently occur in Huon Gulf, Astrolabe Bay and Tami Island art, but their meaning is not known. Schmitz[23] sees here a connection with the myth of Manub and Kilibob; Manub disappears to be reborn afterwards and the double figure represents his dual personality. At any rate, it seems clear that this representation is backed by tradition and only more knowledge will solve this puzzling appearance. There are also other explanations, such as male and female symbolism, fertility representations and other, as the double figure exists in other islands on house-posts, but mostly in New Guinea on lime spatulas,[24] spoons, and on the handles of a number of objects whose meaning is not known (T. Bodrogi, 1961, p. 112, figs. 140, 142, 119, 128). It is well represented in the chalk figures of New Ireland.

In the case of the Buka paddles there are clearly a double head and only one body, or a three-dimensional head and a two-dimensional body, the double Janus head of Greek mythology.

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[22] There is an excellent collection of Kwois in the Australian Museum all having the same type of demon face.

[23] C. H. Schmitz, Zum Problem des Balum-Kultes. Paideuma, Vol. VI, pp. 259-80.

[24] Handles of lime spatulas from the Admiralty Island also show double figures and double heads with only one body. See "Suedsee Expedition": H. Nevermann, Admiralty Island, Bd. III, Halbdd. 132 (21-26).

The shape of the blades in group II is closely connected with the shape of clubs from the east Solomon Islands. There is also a close relationship with the serrated clubs from Rarotonga (Cook Island). It seems therefore, that there is a definite connection between this type of paddle and the clubs so far as shape is concerned, and it is important to note that a few of these clubs have human heads carved on the handle (Guppy: 1895, p. 74). Clubs from New Britain have a conventionalized human head carved on the handle and on the blade, and it appears on the handle of a wooden ceremonial axe from the same district. A paddle from New Ireland also bears a human head in a similar style.[25] This type of head seems to be the same as the triangular one, with the pointed face and the triangular head-dress decorated with flanges, in Buka group II. A similar type of face is to be seen on an unidentified object carved in the round from fern-tree wood, and on a mask, both from the New Hebrides.[26] (Fig. 2, 12-15).

Clubs from the North Pacific coast of the U.S.A. (Boas: 1955, p. 284, ill. 298) show the same combination of sculptured heads combined with geometric design on the blade. There is no stylistic connection between the clubs from the North Pacific and the paddles from Buka, but the same principle is involved in the occurrence of anthropomorphic and geometric elements on the different parts of the same object and the fact that the handle is decorated with a three-dimensional head.

(b) Zoomorphic Motifs (birds, lizards, fish, dogs, pigs, opossums)

The animal most frequently used in Buka decoration is a bird, especially in group I, but it is found only rarely in the other groups. And here we have to distinguish between two kinds of birds, the heraldic, conventionalized bird, and the one in its more naturalistic aspect (pl. 3). The heraldic bird is portrayed as seen from above, with head turned aside, the feathers and spread tail sometimes quite clearly indicated. In group III, however, a few examples (E 8057, E 8052) can be found where the bird appears in its heraldic form[27] or as seen in profile (B 8768 and E 24670, pl. 12) where the bird might be a bush fowl. Bodrogi (1959, fig. 117) illustrates a heraldic bird on a comb from the East Solomons, whilst on paddles from New Ireland a bird is said by the natives to be represented in the wavy lines which form the decoration in the same way as on a paddle from the Admiralty Islands.[28]

In sculpture the bird is represented in a very naturalistic way in the East Solomons on handles of food bowls, in the overall shape of bowls, and on a tie-beam from a canoe house at Uji on St Christoval Island. In New Guinea, according to Bodrogi (1961, p. 162), sculptured birds are occasionally suspended from the roof of club houses and the sea eagle is mostly depicted. The portrayal is fairly standardized but has no resemblance to the bird on the Buka paddles.

Lizards

These are mostly depicted in the same way on the Buka paddles, namely, as seen from above, with elongated bodies, long tail and legs symmetrically arranged (pl. 11). Sometimes eyes are indicated on the head. On E 8063, the lizard is

[25] J. L. Brenchley: The South Pacific Islands, London, 1873, p. 281.

[26] Ethnographical Album of the Pacific Islands, 2nd series by Edge-Partington-Heape, pp. 74 and 135.

[27] There are, however, birds in both described shapes on kapkaps from the Solomon Islands. See G. Reichard, pl. CXXVI and pl. CXXVII.

[28] On kapkaps from the Solomons heraldic birds in profile, and some wavy lines but still showing heads and tails, are recorded. G. Reichard: Melanesian Design, Vol. II, pl. CXXIII, 471, 476-7.

joined on to a kokorra head.[29] Lizards are frequently seen as two and three dimensional decoration in New Guinea. The former is to be seen on the memorial shield (mentioned by Bodrogi, 1961, p. 162 and fig. 70) with circles filled with triangular motifs.

Further to the west we find a sarong decorated with Kauri-application, where a standing spirit is represented between whose legs is a lizard surrounded by fish and circular motifs. There appears to be a connection between the lizards and circular ornaments, as they frequently are associated.

In the Admiralty Islands wooden bowls are found decorated with lizards in low relief.[30] On "dancing-sticks" from Tench Island[31] two lizards, facing each other are depicted, and on another one three fish following each other are represented. They are also used in New Ireland and New Zealand decorative art.

Fish

Fish depicted naturalistically appear in Buka group III (E 8066, E 8047, E 8062, pl. 11) and are in most cases easily recognized as a shark seen from above with eyes, fins and asymmetric tail. Besides these representations we find the shark body with the kokorra head (E 7947, E 7949, E 9780 and A 17055), on which the shark is more conventionalized, but still with its characteristic features, and the kokorra head is also depicted with slight variations.

Then there are the more simplified types of fish found on the decoration of paddles which cannot be easily identified as any particular species, but which I have called the bonito motif, seeing they display some of the characteristics of this fish (B 8001 on pl. 5). On E 7966 three fish are represented following each other in the same way, and in the same style, as on the dancing-stick from Tench Island, mentioned above. No parallels could be found for the frequently occurring motif of the bonito-kokorra (see 8100, pl. 11).

From south-east New Guinea (Bodrogi, 1961, p. 163) the fish motif "appears embossed and engraved on the side planks of houses, on wooden bowls, pumpkin-dishes and coconut cups. It is not always clear what variety of fish is depicted". But sharks are depicted and Mr G. P. Whitley, former Curator of Ichthyology, Australian Museum, told me that shark images are still to be found on the planks of canoes in south-east New Guinea. Bodrogi (1961, fig. 166) illustrates fish decoration of a bowl, in profile with an indication of the gills and with one large eye; on the body is a kind of zig-zag pattern similar to the one carved on paddles with purely geometric design. Fully sculptured wooden fish are used as containers for ashes and bones of the deceased in the Solomon and other islands. This kind of fish, clearly recognizable as bonito, is also to be seen in the Canoe-house from Uji, mentioned previously.

Dogs, pigs and opossums

Dogs or pigs are represented on two paddles in the Australian Museum (pl. 3) and one in the Tasmanian Museum. Greiner (1923, pl. XXIX A,c,) illustrates a dog in profile with four legs and raised tail, carved on a club from Tonga in a more

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[29] On a memorial slab from New Guinea now in the Museum of Dublin a similar representation is to be seen.

[30] Nevermann in "Suedsee Expedition", Bd. III, Admiralty Inseln, p. 203, fig. 117. Also G. Reichard, pl. VII.

[31] Nevermann in "Suedsee Expedition", Bd. II, St Mathias Gruppe, p. 228, fig. 148.

naturalistic way than the animals on the paddles. Fully sculptured naturalistic wooden pigs are to be found on many islands, including the Solomons. Bodrogi reports (1961, p. 163) that "the portrayal of pigs is more widespread in the Bukawa inhabited area, whereas it is quite rare with the Yabims and on Tami Islands". There are only two examples known to Bodrogi of this motif, one on a head-rest and one on a hook, and both are carved in the round.

(c) Geometric Designs

The most frequently used motif in the field of geometric design is the triangle in its many variations and combinations. The triangle is seldom used as a single unit, but mostly in rows, one following the other to form a special pattern, which I called the chevron (see p. 53). There are many ideas about the origin of this pattern, as some see in it fish tails or bird tails; it might, however, possibly have its origin in seeds or shells strung on a string or in another floral model (B 8792, E 7959, E 8099 and others, pl. 13[32]). There is hardly a paddle or wand without the chevron motif, apart from those in group I which have the kokorra head or bird as their only decoration. The chevron is used as a decoration on canoes (Blackwood, 1955, p. 435, fig. 26) and on house beams in the Solomons. Reichard (1933, p. 128) reports the existence of this motif on kapkaps from New Ireland, and on gourds and combs from St Mathias. Further to the west, *the chevron is not frequent in New Guinea*, but it is employed in a similar way to that of Buka on the island of Palau (West Carolines), where Kraemer ("Suedsee Expedition", IIB 3 Palau, fig. 2) shows the same pattern used in the decoration of wooden houses (bois). Kraemer (1932, IIB 5, p. 149, fig. 107a-w), illustrates patterns from Truk Island (East Carolines) corresponding to the chevrons illustrated here on B 8797-1, E 8073-u, B 8783-v, B 8784-w. The pattern of B 8783 corresponds with a pattern found on Palau.

Chevrons also fill the space on the band-like bodies of conventionalized squatting figures, incised as decoration on a club from Byron Straits (New Ireland), illustrated by C. Schuster, (1956-8, fig. 1). This pattern is composed of the limbs of four (or six) squatting figures, whose raised arms form the legs of the figure below. Only four heads are shown. A pattern similar to chevrons, consisting of rows of triangles, is rarely seen in New Guinea but it is used occasionally on drums and clubs. Triangles separated by a band are also sometimes used to fill in spaces according to Bodrogi (1961, p. 172, figs. 227-8).

Triangles, saw-teeth, zig-zag bands

Triangles are used on the paddles to fill in spaces and form special patterns and to indicate feathers on the heraldic birds, scales on fish, or fish motifs. Saw-teeth which represent the teeth of kokorras or their hairline are also used for the framing of the kokorra images on some paddles (pl. 11) and to form necklets. Some horizontal rows of equilateral triangles form patterns by being put vertex to base on the row below, others appear in rows, but are put base to base (pl. 10). In the same way these patterns are used as decoration on dancing-sticks from Truk Island and on spears from the Admiralty Islands (Kraemer, 1932, IIB 5, Taf. 14, c and d), on paddles, clubs and bowls from the Cook Islands (Buck, 1944, pp. 29, 334). A paddle-spear is an example of transition from one style to another (pl. 13). Isosceles and

[32] None of these explanations of origin is satisfactory. Dr Carl Schuster thinks that the chevrons might represent conventionalised bodies of ancestor figures or spirits of past generations, similar to the staffs from the Cook Islands, where the god Tangora is represented sitting on top of ancestor figures. See also the handle of a fly whisk, represented on page 31 in Arts of the South Seas by Linton and Wingert, showing a carved version of the chevrons and on top of these the squatting double figure of a demon or spirit.

flanges, i.e., triangles with curved side lines, are also used on paddles from the Buka district (unnumbered on pl. 13) and on the head-dress especially of carved kokorra heads in Buka group II. The same kind of pattern is to be seen on some unidentified implements from the Admiralty Islands (Nevermann, IIA, 1932, 3, p. 388, ill. 277-8). E 8100, which is club-shaped, is butted at the end and rather heavy, also shows the same pattern. Saw-teeth motifs and isosceles are frequently used in south-east New Guinea on bracelets, and also by the Bukava and Yabim tribes on house posts and almost all kinds of carvings (Bodrogi, 1961, p. 128 and figs. 175-80).

Zigzag bands

A very interesting pattern is formed by using the zig-zag band in a specific way, as on B 8809, which shows on one side the ordinary chevrons in different shapes with the kokorra head, and on the other side the zig-zag band, starting with a loop on the point of the blade and running to the end of the paddle, which has no division into blade and handle, but is fish-shaped without a pronounced handle at all, becoming narrower at the end. B 8786 is the same shape, but unfinished, without any decoration on one side; it has the same zig-zag band on the other side as on B 8809, but running in the opposite direction (pl. 14). The loops on both paddles are painted alternately black and red on a white ground. B 8786 (pl. 14) shows the motif framed, as there is an edge carved on both sides of the paddle and in between the zig-zags, the loops becoming bigger on the widest part and smaller on the narrowest portion. Both paddles are well carved and executed.

On no other paddle could I find the same motif, which is quite common on canoes in the Buka district. A special plank called watsinan, let in at the end of the mon plank canoe above the water level, carries this pattern and Blackwood (1935, p. 378, pl. 25B) shows a native carrying the watsinan decorated with the zig-zag band exactly in the same way as on B 8809 and B8786. Figure 26, p. 435, in Blackwood, shows the pattern combined with kokorras and kokorra heads and chevrons on planks used for building boats. It seems, however, that this pattern is quite common on other islands and in north-east New Guinea. It is found incised on gourds from St Mathias and also on spears, on dancing-sticks from Emir, as well as on combs from Sumba (Reichard, 1933, pl. CXLI, 594-8, and Parkinson, 1907, pls. 19-20). The zig-zag band is frequently seen on objects from New Guinea, especially from the Huon Gulf area, the Bukava district and on Tami Island. The motif is used to decorate the bodies of snakes carved on clubs and drums, on bull-roarers, to indicate the bones of fish, and on wooden bowls from Tami Island. (Bodrogi, figs. 50-1 and fig. 159, also Reichard, 1933, pl. LXXV.)

Circles

Another motif quite frequently occurring on the Buka paddles and wand, is the circle, which is also connected with the saw-teeth ornament and the triangles as many of the circles are filled with these patterns. There are three types of circles, firstly the one consisting of concentric rings filled with saw-teeth lines and divided into sections, secondly the circle filled with floral motifs such as flower petals, and thirdly, the circle with a whirl like the limbs of an octopus or a star-fish. Bodrogi (1959, p. 32, fig. 95) shows these circles, filled with exactly the same ornaments as on the paddles and some kapkaps. On a wooden board from a house in North Ireland, the carved figure of a spirit in the centre bears the circle filled with ornaments on his breast. The circular motifs to the right and left of the figure show the division into sections, concentric circles in the centre surrounded by bands filled with chevrons and straffings and a halo formed of flanges around the outer contour. We find this kind of filled circle on E 7981 (pl. 7) of Buka group III, where a kokorra sits on one

circle, divided into sections, followed by a band of saw-teeth and an outer circle. The motif is simplified in the carving on the paddle and more elaborately executed on the wooden board from New Ireland. B 8752 (pl. 5) in group II shows an oval carved in openwork underneath the double-headed handle part, and the same motif, also divided into four sectors, but this time more circular shaped on the blade, surmounted by a kokorra head. Another paddle of this group, E 6513, shows the motif twice on the part underneath the carved head, and the kokorra on the blade has two concentric circles with a centre dot carved on his breast painted in the usual colours. See also Bodrogi, 1961, figs. 177-182.

The fully sculptured figures from Buka (McCarthy, 1951, p. 182-183) show the same circular motif divided into sectors on their breasts and painted in the same colours as on the paddles. Bodrogi (1961, p. 170, fig. 224, b and c) illustrates similar motifs, though not divided into sections, which consist of concentric circles, surrounded by saw-teeth bands.[33] These circular motifs are also used on ornaments called kankan, made from turtle shell and pearl shell, and sometimes of thin sheets of wood. These ornaments are worn by the natives of the Bukava, Yabim tribes, and on Tami Island on festive occasions, tied round their necks or on their foreheads, and they are often seen on the chests of young children, probably as a kind of protective talisman. This is most probably also the meaning of the kapkaps. Bodrogi says further that the circular motif is mostly used on bracelets and coconut cups but less on wooden carvings, but it occurs on gourds from St Mathias (Reichard, 1933, pl. CXLI), and on carvings from New Guinea.

We then find the circle filled with floral decoration in the shape of petals of poinsettias. This plant has been introduced by the Europeans to the islands of the Pacific and is thriving in these areas. The motif is used sometimes in asymmetrical form on E 8057 and also asymmetrically on E 7985 and B 8914 (pl. 14). The latter is from New Britain and not the Buka district. The symmetrical circle might be filled with from 7 to 14 petals on paddles in group III (B 8788). A similar circle filled with petals and also divided into sections, is to be seen on a wooden house shield from Telei Island (Bodrogi, 1959, pl. 120). Circles filled with floral motifs also appear on painted paddles from Mangpaio (Cook Islands) and on a ceremonial paddle from Hervey Island.

Lastly we find the circle with a whirl motif consisting of limbs of the star-fish or octopus, or in the shape of coils, as on E 7981 (pl. 7) where the first type of circle is also to be seen. No parallels to this motif could be found anywhere, except Indonesia.[34]

Very rarely concentric circles are found and there exists no spiral on all the paddles I know from the Buka district. The motif with voluted ends, or a coil with one and a half turns, previously mentioned on paddles B 8796 and E 7974, is believed to represent a woman's breasts (pl. 6). The arms of the kokorra sometimes end in voluted ends, instead of hands, which, by the way, are mostly indicated by three or four digits, seldom by five, sometimes by as many as six or seven. There is another motif, which Reichard (1933, p. 132, fig. 65d) describes as "an adaption of the typical Admiralty Island two-and-a-half-turn spiral"; it occurs frequently on paddles in all Buka groups.[35] (E 7968, pl. 6.) It is to be seen on one side of E 7930 (on the other side is a kokorra on a stand which occasionally shows voluted endings) and on E 8057, E 8088 and E 7968 to fill in spaces (pl. 6). As a scroll this motif is found on E 7985 (pl. 13) and on the decoration of paddles from New Zealand.

[33] Bodrogi: 1959, pl. 51, shows a bamboo case decorated with the same motif above a conventionalized bird and a demon face from Tami Island.

[34] See S. Kooijman, Ornamented Bark-cloth in Indonesia, figs 12, 13, 197.

[35] This motif occurs frequently on gourds and bamboo containers from the Admiralties and on carvings of all kinds from New Zealand.

Concentric designs and odd patterns

Geometric rectilinear patterns are mostly to be found on paddles in Buka group II on that part of the paddle just underneath the carved head. On page 43 it was said that these patterns were similar to the patterns used for tattooing and that their position corresponds with the part of the kokorra's body, which is usually depicted underneath the kokorra's head, so that one could assume that instead of a naturalistic we have a symbolic representation.

These concentric patterns are mostly rectilinear in style and their shapes are adjusted to the space to be filled, so that a wide variety of shapes is to be seen. These patterns are painted in red and black alternately on a white ground, or red and black only. Bodrogi (1959, pl. 14) shows a wooden shield from north New Guinea where the same motif occurs, namely, concentric shapes engraved on a spirit's head, but, in contrast to the patterns on the paddles, the white ground forms the pattern, whilst in the Solomons, although the ground is also painted white, the pattern carved in slight relief and painted red or black forms the decoration. Concentric patterns are also to be found on kapkaps from south New Guinea (Reichard, 1933, pl. CXIXVIII). Bodrogi (1959, pl. 108) represents a mask from Witu Island (Bismark Archipelago) showing concentric rectangles carved in slight relief and painted red and blue on a white ground in the same way as we saw on the paddles. Another mark from Nissan Island shows this pattern as a tattoo on the face (Bodrogi, 1959, pl. 113). A carved pole from the New Hebrides bears concentric squares, used diagonally as a decoration on the figure's breast (Bodrogi, 1959, pl. 123). Greiner (1923, pl. IVa) represents concentric rectangles in the decoration of a wooden bowl from the Marquesas.

There remains one paddle to be discussed, which shows purely geometric decoration. It is E 7971 (pl. 14) which has an intricate pattern carved in slight relief on both sides, formed by placing two strangely shaped elements in opposite pairs. They are painted red and black alternately on a white ground. Through their shape and the way these elements are placed a very regular, symmetric pattern of stars appears on the paddle's white ground. The alternately black and red shapes are also to be seen on the kapkaps from the Solomon Islands (Reichard, 1933, pl. CXXIV, 482-4), placed in rows or bands round the centre of the kapkaps, which is divided into sectors. Very few instances are known to me where a pattern of stars is formed; one is on a carved door-jamb from a house in New Caledonia, where the star-pattern is formed by angled concentric lines. (R. Linton and S. Wingart, 1946, p. 79.) Another example of a star, formed by concentric lines and geometric designs, is to be seen on a bark belt from the Gulf of Papua, where the centre of the star is marked by three concentric circles. The geometric design represents a double row of conventionalized faces and a naturalistic lizard is placed in the centre of the whole pattern (Haddon: 1895, fig. 14).

From all that has been said in the above chapters about the distribution of identical or similar motifs and patterns which occur on the paddles and wands of the Buka district and in the different island groups, one can conclude that there is no individual pattern belonging exclusively to the Buka paddles, it is in the use that is made of these patterns and the special way in which the motifs are emphasized, combined and spaced that the individual style of that district is expressed. There is more individuality to be found in the shapes of the paddles than there is in the kind of decoration. The most individual feature, however, is the kokorra figure as seen in profile, and the way a woman is indicated by her breasts in contrast to a man, if the representation of the flourish emanating from the head is correctly identified. Then there is the framing of scenes on the paddles and wands and the indication of landscapes or huts. The representation of birds, especially in profile, is unique to the art of Buka.

4. STYLISTIC OBSERVATIONS AND CHARACTERISTICS

Following the observations of Franz Boas[36] on primitive art and employing the same analytical methods on the paddles and wands from Buka, it is apparent that the Solomon Islanders followed in principle the evolution that most primitive people have achieved. As the paddles do not represent a beginning but an acute state in the evolution that has taken place through the centuries, we find many elements belonging to different stages of evolution and also to different cultures, mixed together to form a new style. This is mostly expressed in the combination of the representational and geometric styles in both rectilinear and curvilinear techniques. The ceremonial wands are as a group homogeneous in their decoration; the same principle of symmetry is used with few exceptions. There is no evolution to be found, only differences in applying the same motif in various forms, from the more traditional representations to a more liberal use of the human figure. The same principle implies also to the zoomorphic motifs. We have seen birds depicted in a heraldic way on some examples and more naturalistically on others. And in the same way fish are represented naturalistically and sometimes conventionalized and reduced to patterns.

As Boas (1955, p. 69) pointed out, "neither primitive man or child believes that the design or the figure he produces is actually an accurate picture of the object to be represented. He may represent a human figure in utter disregard of detail and concentrate on the essential features which are important to him, or he may give details in a realistic representation and disregard the form as a whole". We find both these kinds of representations on paddles and wands. The figure of the kokorra is usually shown in a symbolic traditional way with an enormous head, and the eyes, nose and mouth indicated only by outlines, the ears always represented in the same distended way and the body as seen from the front. It is a flat, two-dimensional, symmetric-geometric, unpersonal kind of symbolic representation.

In human figures in profile, however, we could find a kind of development in so far as, for once, somebody tried to produce a more naturalistic impression of a man; the other artists liked the idea and tried their hand at it, too, each adding something, so that a more individualistic and asymmetrical figure appeared. Some of the figures in profile look like an ordinary kokorra cut in half, whilst gradually a figure in profile is to be seen, which fits properly into the given space and has a naturalistically moulded back-line. Some of the spirits carry an axe, some are seen as sitting on a stone (?), others are shown as in movement (pls. 8 and 9, E 8057 and B 8759). All these figures show the body in profile, but the head in the usual manner. It seems as though the head of a spirit or ancestor figure, imbued with the most symbolic meaning, was the last feature to be changed and there are only a few paddles or wands where the head is also shown in the profile (pl. 15), which proves that in the development of a naturalistic representation the symbolic representation has been of fundamental importance.

Both kinds of representations are based on a distinct mental attitude and different psychological sources and might not have been found together in a more primitive time, but, at the stage of mental development when the Buka ceremonial wands originated (approximately at the middle of the 19th century), so many different traits had been assimilated that no pure style could exist any more.[37] Therefore

[36] Franz Boas, Primitive Art, New York, 1955.

[37] C. A. Schmitz stated in Historische Problem in N.O. Neuguinea, Studien zur kulturkunde, Vol. 16, 1960, that curvilinear two-dimensional surface delineation belongs to the round adze culture, whereas purely geometric ornamentic is the work of Austronesian migrants. To the southern Austronesian culture also belong the angular forms of human representation with arms hanging down, block-shaped shoulders, hips, feet; this holds good for other parts of Oceania and the Solomon Islands.

there is the occurrence of such different art expressions, not only in the various groups of paddles and wands, but also on one object. And that brings me to another point; not only do we find anthropomorphic, zoomorphic and geometric decoration on almost all paddles and wands, but the way these patterns are designed shows two different styles combined, namely the rectilinear and the curvilinear. The body of the kokorra may be angled and the rectilinear character of the design might be emphasized, whilst on another kokorra on the same specimen the figure might show rounded outlines and the geometric decoration might be in either style. But if we consider on how many groups of islands we find the same motifs used, though in a different way, as each island of a given group might have developed its own characteristics, and if we realize that close communication must have existed all the time, the resulting diffusion of styles is understandable. Besides, there are craftsmen and artists in all form of societies; some rise above the level of the skilled artisan and tradesman who were satisfied with imitating the existing patterns. "Carving in wood, bone, ivory or stone, and modelling in clay are the principal arts that give freedom to the artist", says Boas (1955, p. 85), "which is not so easily found in graphic representation." That is also true of the Solomon Islanders, as their sculptured figures are naturalistic and show a variety of postures and individuality compared with the more unified of the two dimensional representations on the paddles.

Boas thinks that style has the power of limiting inventiveness; although artists work without copying their imagination never rises beyond a certain level for they merely reproduce familiar motifs, composed in a customary way. In the decorative field, however, even if forms and elements of patterns are identical, as we found them in the chevrons and the zig-zag lines or saw-teeth bands, or the triangular shapes, it is the arrangement which gives specific form to the art of the each locality. The style of the Buka paddles and wands is so uniform that it can quite easily be recognized by its characteristics.

Each of the three groups of paddles and wands has its special characteristics, but all show the same type of spirit figure or head with the same head-dress or hair-do, which is onion-shaped or like a halo, the special way of representing nose, eyes and ears. There is very slight variation in the features, but the difference lies in the arrangement of the single motif and especially in the spacing on the blades. Paddles and wands from group I and II show a single motif such as a bird or fully figured kokorra or a kokorra head occuping the centre of the blade. It is on the wands from group III that the greatest variety of motifs are used, and here, too, the given space is never overcrowded, the single motif is always well placed to cover all the available grounds. It may be elongated when necessary or spread out to a certain degree, and there is always space left for framing. And this is an important characteristic of the group: there is a narrow band, sometimes finished off by a tooth-line, running along the edge of the kokorra, getting wider where more space is available and narror if ther is little space left (E 7981 and E 8056 and also E 7974 and E 7950 on pls. 7, 8 and 10).

Then we have the interesting example E 8053 (pl. 8) which shows the most elaborate framing of all the wands, the framing is not only asymmetric, as is the figure represented, but it also forms part of the action. The kokorra is a curious mixture of profile and frontal representation. The head is as usual seen from the front, the body is in profile, with one arm only and one leg on the oposite side of the body and an axe growing out of its shoulder. The creature seems to sit on an unidentifiable object, which forms the body of one kokorra pointing in the opposite direction. The framing reminds me of a landscape setting, being given in three lapped shapes pointing once up, once downwards. There is always enough space left for the ground between the motifs to show the light wood-coloured ground, or

the ground is painted in white from which the pattern emerges either in the dark wood colour, or is painted red or black. This gives the decoration its special, more sophisticated, lively appearance, in contrast to the more overcrowded decoration from other islands. Even the paddles decorated with purely geometric ornament show the same quality. The great variety of motifs and their specific combination add to the character of the Buka paddles and wands.

The outlines of the designs are closely drawn with a sure hand and a good sense of rhythm. It is not lines which count in the overall design, as for instance, in New Guinea art; it is more the lines as contours that give value to the enclosed planes. (Pl. 14, as on B 8766, E 7971 and B 8786.)

The fully sculptured double or single heads on the paddles in group II are constructed of planes, which meet at an angle to form a ridge, so giving the face a ferocious, barbaric, animal-like appearance (pl. 4, B 721). The contour of the profile is very simple, cubistic in its angular outline, as there is hardly an indication of nose or mouth to be seen, only the big round indication of an eye. In the second type of head, the two faces are formed by two triangles joined together by the hair-do, which also forms a vertical ridge in the same way as the two triangular shapes which form the faces (pls. 4 (B 721) and 5).

5. CONCLUSIONS

Summing up what has been said in the previous pages, it could be stated that the ceremonial wands from the Buka district follow in their overall shapes and decoration the general pattern of development common to the different island groups, each in its special way; combining and modifying the motifs, which are the heritage of innumerable generations of tribes and peoples which have come most probably from the mainland of Asia and populated the whole of the Pacific Area.

Even the motif which I thought at first would be an addition of more recent times, the upright kokorra figure, seems to go back as far as the kokorra in the position of adoration, which is one of the oldest and most widely distributed motifs in the whole of the Pacific Area. There remains only the figure in profile and carrying an axe, for which I could not find any parallel, which might be an addition more or less genuine to the Buka district. All the other features could be accounted for in one or the other island groups, mostly New Guinea. Even the way the nose, eyes and eyebrows are designed has a parallel in the incised bone drawings and wooden sculptures of the Pi-wan tribes in Taiwan, but nowhere could I find a creature like the one on E8059 (pl. 15) seen in profile, sitting quite leisurely and carrying an axe. Only three of these figures in profile, with the head in profile as well, have come to my notice, but some of the kokorras in profile with frontal heads are also exceptional in carrying an axe (pl. 8, E 8081, E 5346 and E 8053). E 5346, which shows the same naturalistic sensitive contours as E 8059, differs from it in having the head depicted in the conventional way. It is remarkable that all the figures carrying an axe are seen in profile, and there is only one kokorra standing upright in profile (pl. 9, E 24669), but with head in frontal view. The embryo-like creatures without head-dress are in profile, (B 8905, pl. 5) and the one with head in frontal view on B8775 (pl. 8). All these figures are shown in a static position, but we find a few animated figures in motion on E 7949, B 8759 and E 7951 (pl. 9).

We then have a variety of kokorras in different shapes, but this is more a playfulness on the part of the artist than the creation of a new type, as it is the usual figure abbreviated, the body transformed into an ornament to fit into the available space (E 8004, E 8046, E 8036, E 8077, E 8783 and E 8763).

B 738 (pl. 3), with the two pairs of animals standing opposite[38] each other, is also an exception to the usual pattern, and no parallel could be found in the immediate surroundings, except on some of the wooden carvings from Taiwan (Chen Chi-Lu, 1961, 122, ill. 121-123) and in mainland China.

The representations of birds, either in a heraldic way or in profile, somewhat naturalistically, is more or less confined to the Solomon Islands and also to the Pi-wan group of Taiwan, the islands of Indonesia and the Easter Islands.

Most of the elements of the geometric ornamentation could be traced back to Indonesia, New Guinea or the different surrounding groups, although some of the more elaborate patterns are unique and are only found in the Buka district (pl. 14, E 7971 and B 8766).

The framing and spacing are also very characteristic for the Buka district and give the decoration of this locality its special flavour.

Another conclusion to be drawn from the prevalence of the anthropomorphic element over the geometric in the decorative art of Buka is that the Solomon Islanders were greatly concerned with head-hunting and cannibalism and this might explain their preoccupation with the human motif and the ancestor figure. Another fact might also be important in this connection, namely, that the wands in group II, whose shape could be traced back to that of clubs, shows as their main decoration the spirit head double or single, fully sculptured. It could be shown that clubs mostly carry as decoration spirit heads in other islands and that clubs from the North Pacific coast of America use the spirit head fully sculptured on their handles.[39] It seems that the club meant to smash the enemy's skull bears significance in this respect to the decoration.

It could be said that nowhere else is there to be found such a variety of shapes as in the wands of group III as ceremonial implements. There are island groups where a variety of types of ceremonial spears is used, and the dancing-sticks of the St Mathias Islanders are in a variety of different shapes. The ceremonial paddles of New Zealand, the Cook Islands, the Carolines, New Ireland and New Guinea have not developed a separately shaped paddle for dancing purposes; they used the existing shapes more elaborately decorated, more richly carved and painted. It seems, therefore, that the great variety of shapes in the ceremonial wands from Buka is another characteristic development of that area. The various shapes of wands in group III include a number of features partly from other island groups, partly from other ceremonial implements, such as ceremonial spears and clubs, and there are many examples of traditional shapes to be found. The paddles and wands thus show features of several types united in one or the other paddle and wand from the three Buka groups, in all of which the art forms are interrelated. The same could be said of the decoration: although different types of patterns, characteristic for one group of paddles, could be established, as the heraldic bird for group I or the tattoo patterns for group II, there are also several examples from group III showing this special decoration.

The geographic fact that the Solomon Islands are very centrally situated and are so near to such rich artistic centres as New Guinea might account for the variety of shapes, and also for the special character of the decoration, uniting different elements to form new and very complex patterns of artistic expression.

[38] This, too, is one of the oldest motifs in Asia and found its conventionalized form in the Tao' Tie' of the Chang Bronzes, 2000 B.C. See also the very interesting article by R. Heine-Geldern: L'art prebouddhique de la Chine et son influence en Oceanie, Revue des Arts Asiatique, Tome XI, 1937.

[39] Franz Boas, Primitive Art, fig. 298, p. 285. See also club handles from the Marquesas, in the Oldmann Collection of Polynesian Artefacts in Supplement to the Journal of the Polynesian Society. Memoir No. 15, Instalment No. 10, pl. 92-96.

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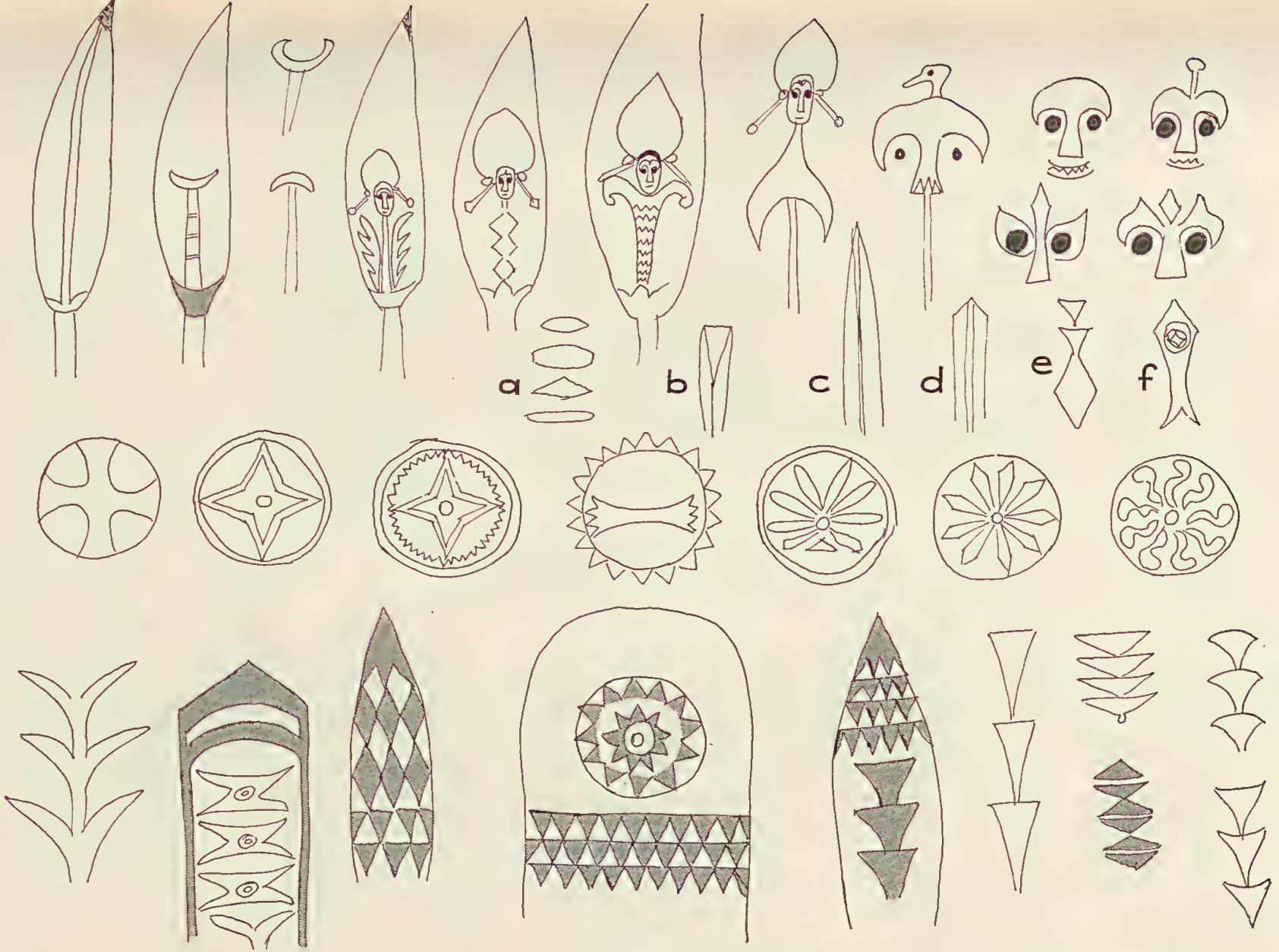


Figure 1

Top Left: five paddles decorated with different types of heads on stands, and, between the second and third paddles, stands only. Top right: further types of decorations on stands and different types of eye motifs resembling birds. (a) Cross-sections of four paddles; (b,c,d) profiles of paddles; (e&f) variations of the fish motif. Centre row: circles filled with different decorative motifs. Bottom row: centre, a stone at Iltopan, north-east Bougainville (after B. Blackwood), and, on each side of it, paddles decorated with similar triangular motifs; the paddle on the right of it is also decorated with chevrons. Extreme right: five variations of the same motif on other paddles. Extreme left: two decorative motifs on paddles, possibly of naturalistic origin.

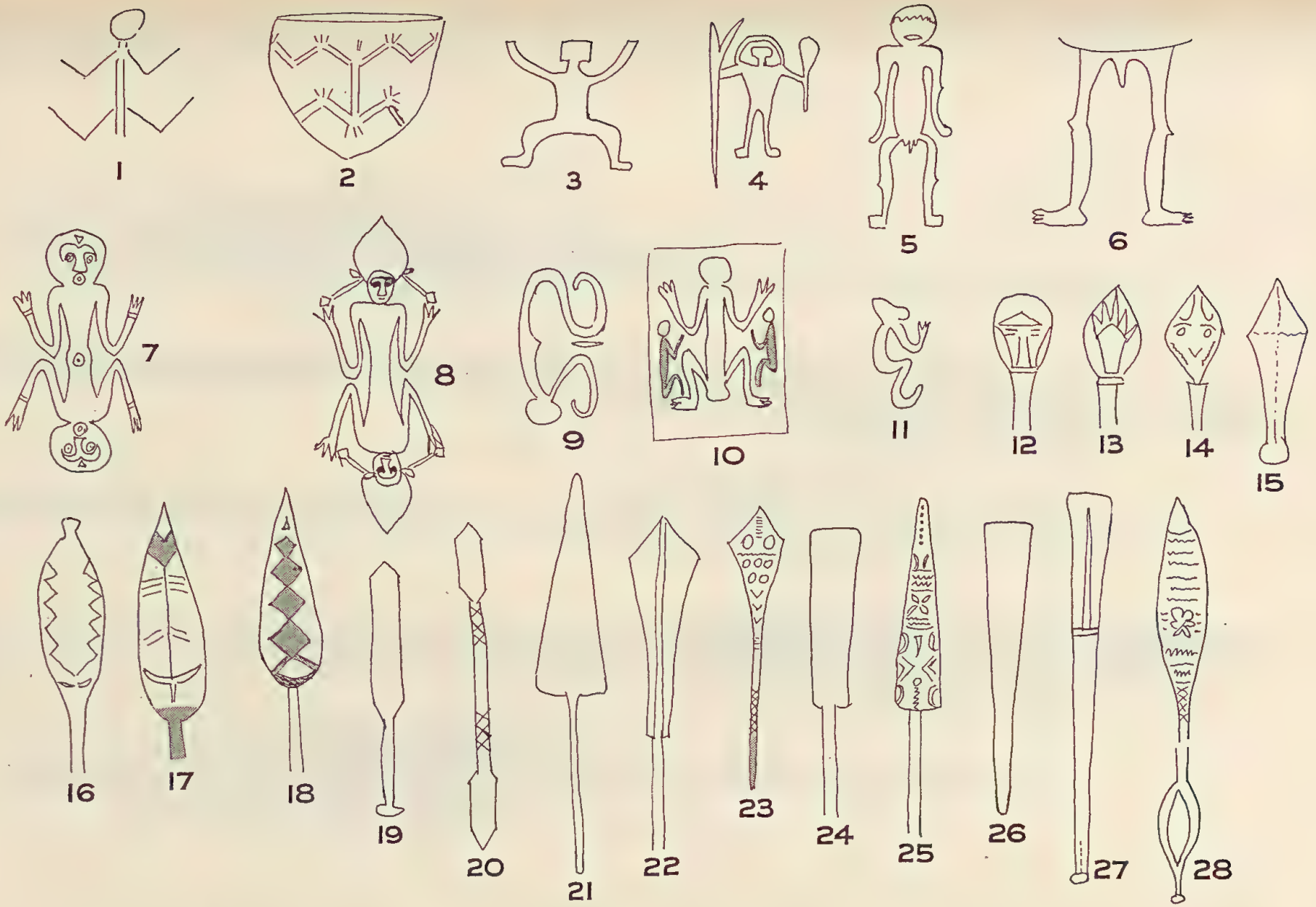
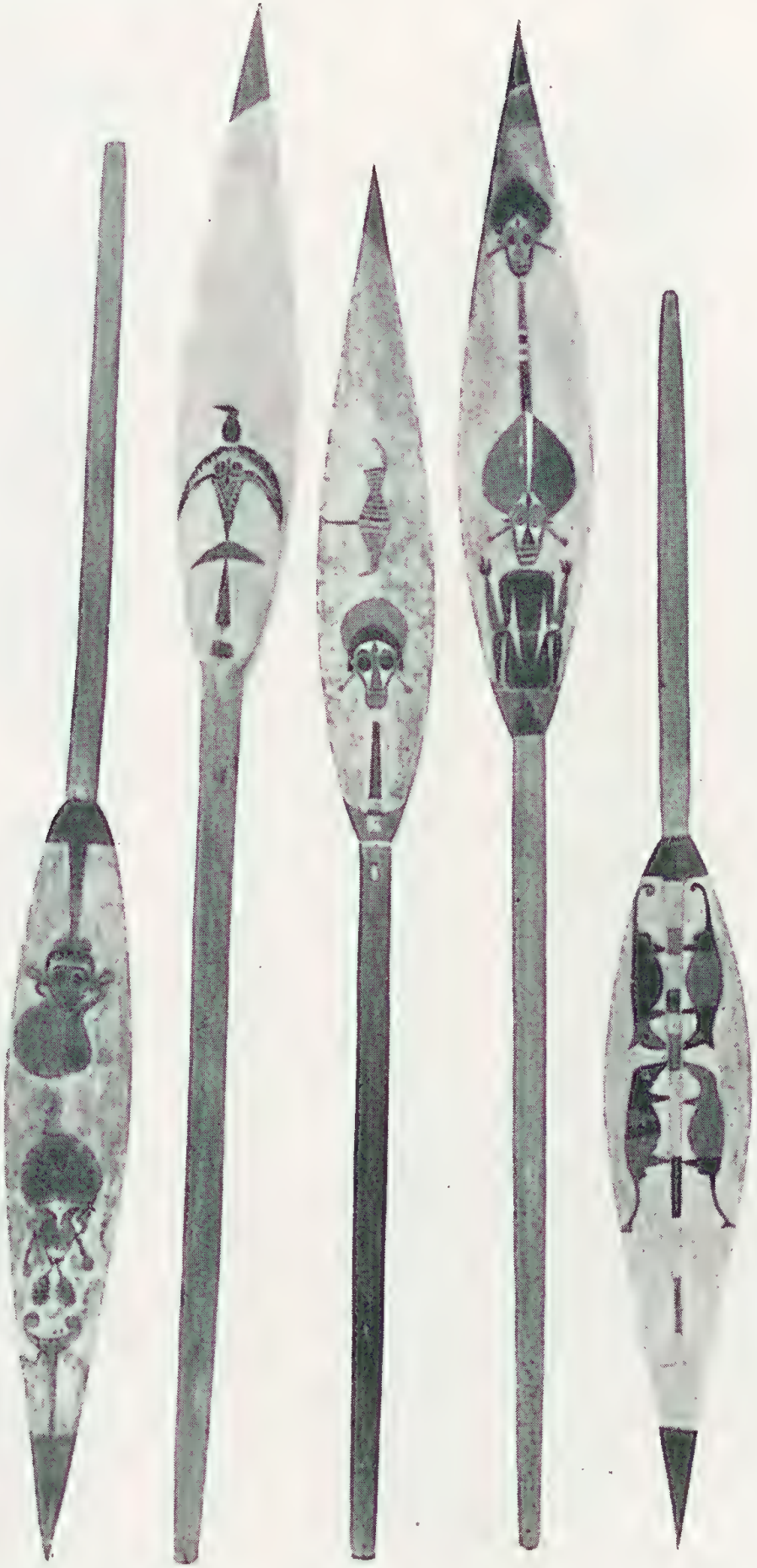
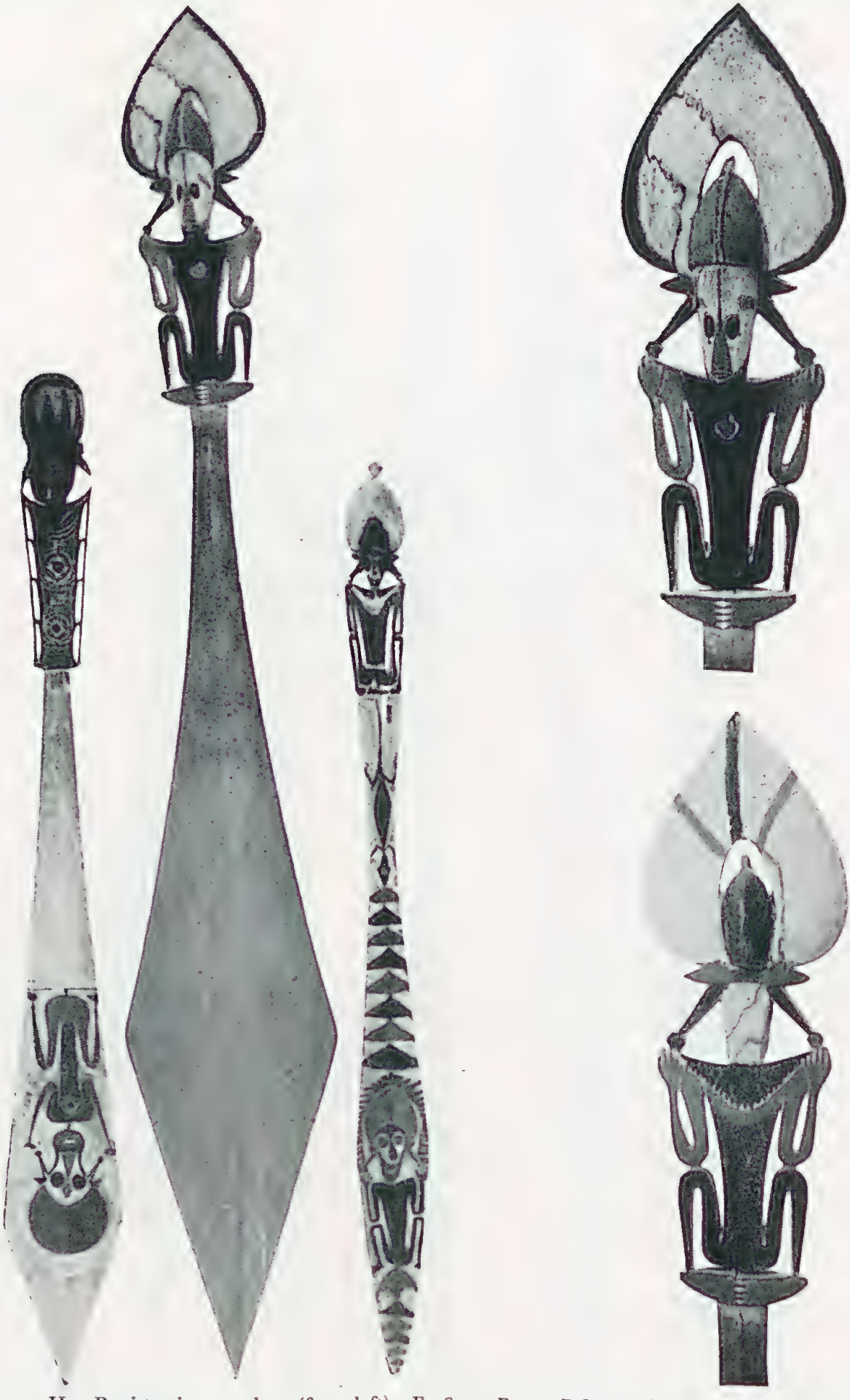


Fig. 2.—1 and 2, after A. Lommel, China. 3 and 4, after R. Greiner, Marquesas. 5 and 6 after R. Linton and P. Wingert, Indonesia. 7, after Chen Chi-Lu, Formosa. 8, Paddle, Nos. E8001 and E8102. 9 and 10, after A. Lommel, New Guinea. 11, petrograph from Hawaii. 12, 13, 14, 15, clubs from the New Hebrides. 16 and 17, paddles from Palau. 18, 19, 20, paddles from Micronesia. 21, 22, 23, 24, paddles from Cook Islands. 25, paddle from St. Mathias. 26, 27, 28, paddles from New Zealand.



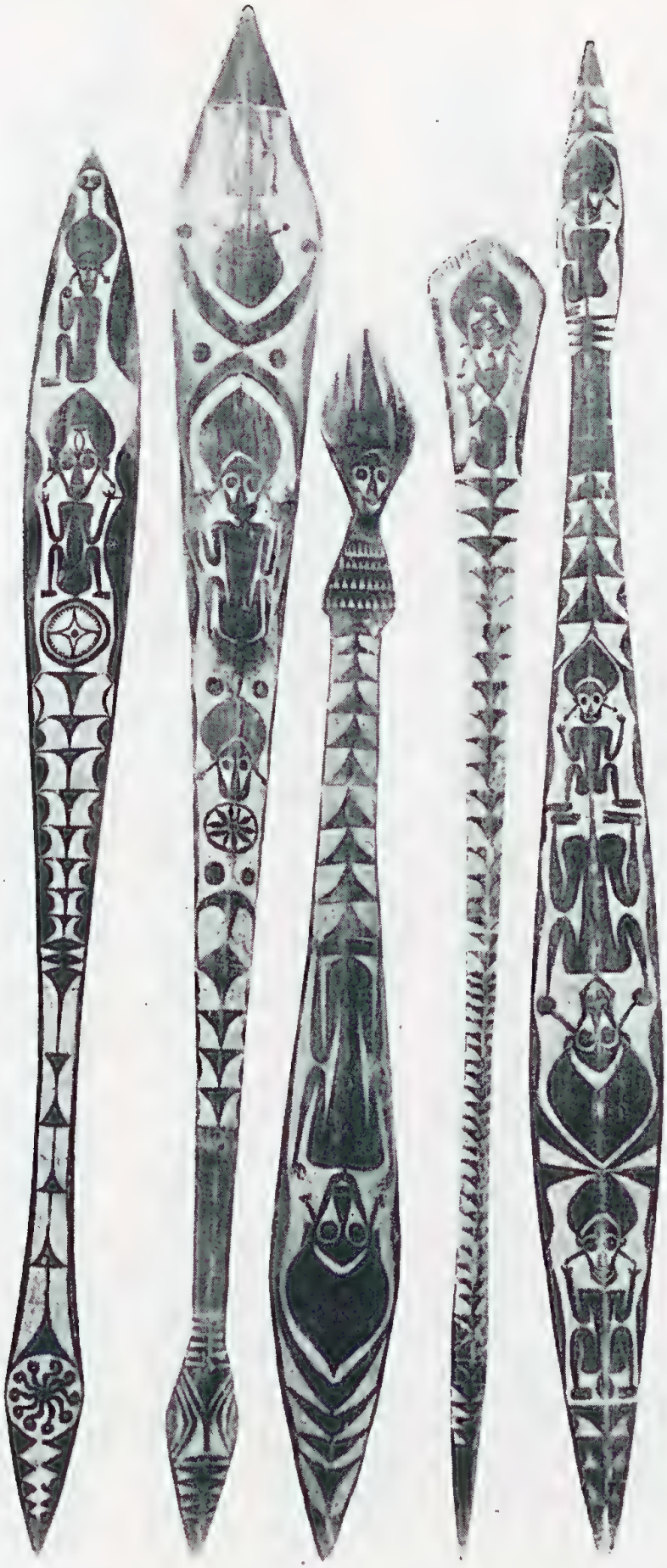
Group I.—Registration numbers (from left): Unnumbered, E 1159, B 8722, B 8755, B 738.



Group II.—Registration numbers (from left): E 16513, B 721, B 8740; detail of top of B 721 from front and behind.

Groups II and III—Registration numbers (from left): E 8037 B 8752, B 8905, B 8921, E 8001.

Group III—Registration numbers (from left): E 8785, E 7968, E 26516, E 8049, B 8796, E 7974.



Group III—Registration numbers (from left): E 7981, E 8057. B 8758, E 8080, E 7950.

Group III—Registration numbers (from left): E 8084, B 8081, B 8775, E 5346, E 8059, E 8053.

Group III—Registration numbers (from left): E 7952, E 7951, B 8759, E 24669, E 7995, E7955.

Group III—Registration numbers (from left): E 8052, E 24668, E 8079, E 8056.

Group III—Registration numbers (from left): E 8100, E 7966, E 8063, E 8061, E 7947, E 8062.

Group III—Registration numbers (from left): B 8749, E 8048, E 24670, B 8768.

Group III—Registration numbers (from left): E 7985, B 8896, E 7959, unnumbered, E 7990, B 8784.

Group III—Registration numbers (from left): B 8786, E 7971, B 8766, B 8914.

Details of E 8059 (plate 8).

Notes on some Australian and New Zealand Stomatopod Crustacea, with an Account of the Species Collected by the Fisheries Investigation Ship *Endeavour*

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Figs. 1-10

Manuscript received 29th January, 1965

G 13246—1

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ABSTRACT

Observations are presented on several small collections of stomatopods from Australia and New Zealand. In all, 24 species in 10 genera are reported, with the treatment of individual species varying from a brief listing to a complete redescription. A key to the 14 genera known from the area is presented. The New Zealand and Australian species of *Heterosquilla* are redescribed, and one new genus, *Hadrosquilla*, and two new subgenera of *Heterosquilla*, *Austrosquilla* and *Heterosquilloides*, are recognized. A new species of *Manningia* from Australia, *M. notialis*, is described. *Gonodactylus platysoma* Wood-Mason and *G. smithii* are resurrected from the synonymy of *G. chiragra* (Fabricius). It is shown that *Squilla inornata* Tate is not synonymous with *S. perpensa* Kemp, as previously believed, and that *S. anomala* Tweedie is a synonym of *S. perpensa*. Synonymies for the few New Zealand stomatopods are brought up-to-date. The references include most of the papers published on adult stomatopods from the Indo-Pacific since 1941.

INTRODUCTION

This paper was originally planned as a short report on the stomatopods collected by the ill-fated Fisheries Investigation Ship *Endeavour* in Australian waters between 1909 and 1914. The *Endeavour* collection, although small, includes specimens of two rare species, *Squilla foveolata* Wood-Mason and *Odontodactylus cultrifer* (White), as well as a large series of *Hemisquilla ensigera* (Owen).

It was then decided that this would be an opportune place to include remarks on the small series of stomatopods obtained from northern Australia by the joint U.S. National Museum-Australian Museum Expedition to Arnhem Land in 1948, hereafter referred to as the Arnhem Land Expedition. This collection included two species of *Gonodactylus* as well as an undescribed species of *Manningia*.

In the early stages of preparation of the manuscript, several letters relating to it were exchanged with J. C. Yaldwyn, of the Australian Museum, who encouraged further expansion and who made available, on loan and exchange, representatives of several species which I felt required further study. These included the specimens of *Gonodactylus* that Stephenson and McNeill (1955) had suggested were near *G. platysoma* Wood-Mason as well as specimens of the six species of *Heterosquilla* that had been recorded from Australia and New Zealand.

Our knowledge of the Indo-Pacific stomatopod fauna stems mainly from the excellent monograph published by Kemp in 1913, supplemented by many papers of more restricted coverage that have been published since that time. That his paper is still the standard reference work is a tribute to Kemp's thoroughness, accuracy, and good judgment. The respect for Kemp has been so great, however, that many subsequent workers have accepted his findings without question and have shown reluctance to re-examine his conclusions concerning several difficult problems. For example, many "variants" in *Gonodactylus* are referred to *G. chiragra* (Fabricius), and *G. platysoma* Wood-Mason has continued to be treated as a "variety" of *G. chiragra*. Additional problems in *Gonodactylus* and other genera have been ignored and Kemp's treatment has seldom been questioned. As shown below for *Gonodactylus*, which is one of the most difficult stomatopod genera, several recognizable species have been relegated to *G. chiragra*.

A similar situation exists in the Pacific species of *Lysiosquilla*. *L. maculata* (Fabricius) and two varieties, *sulcirostris* Kemp and *tredecimdentata* Holthuis are presently recognized. All three of these are actually distinct species, differing not only in

morphological features but in colour pattern. In addition, there are at least two undescribed species involved in what is now called *L. maculata*. All of the Pacific species of *Lysiosquilla* need to be restudied in detail.

In their key to the Australian species of *Lysiosquilla*, Stephenson and McNeill (1955, p. 246, footnote) note that "it seems doubtful if this variety [*sulcirostris*] is distinct from the '*forma typica*'." In my opinion, there are good reasons for recognizing *sulcirostris* as a distinct species; it may or may not occur in Australia.

It is also Kemp's authority that until recent years has stabilized the generic nomenclature of the stomatopods. Kemp's influence has been so great that some authors have argued that genus A was closely related to genus B because it was next to that genus in Kemp's key, even though Kemp himself made little attempt to show interrelationships of genera. Recent work, by Serène (1962) on *Pseudosquilla*, Manning (1963) on that genus and *Lysiosquilla*, and Holthuis (1964) on *Gonodactylus* and the *raphidea* section of *Squilla*, has shown that many of the old, accepted genera were composites. As several important generic changes have been proposed since the last major work on Australian stomatopods was published (Stephenson and McNeill, 1955), a key to the Australian genera is included here. Genera not further treated in the present paper are set off in brackets.

Inasmuch as no further work on the Australian stomatopods is currently planned by the present author, it seems best to include here observations on miscellaneous specimens from Australia examined in American and European museums.

The Australian Stomatopoda have been studied in some detail in recent years, primarily by W. Stephenson, of the University of Queensland. As a result of his efforts the Australian fauna is one of the best known in the world, perhaps second only to the Indian fauna. Some sixteen species were recorded from Australia by Kemp (1913); at the present time this number has increased to forty-eight. A further increase can be expected, for the present work clearly shows that there is still much to be learned about the Australian stomatopods, particularly in the genus *Gonodactylus*.

Fourteen genera, including a new genus described below, are known to occur in Australian and New Zealand waters, and species in ten of them are treated in this report. Species in two of the remaining four, *Pseudosquilla ciliata* (Fabricius) and *Lysiosquilla maculata* (Fabricius), were discussed by Stephenson and McNeill (1955), but representatives of the remaining two genera, *Mesacturus* and *Acanthosquilla*, were included by them under different generic names, *Gonodactylus* and *Lysiosquilla*, respectively. *Mesacturus* is represented in Australia by *M. spinosocarinatus* (Fukuda), and *Acanthosquilla* by *A. acanthocarpus* (Miers) and *A. multifasciata* (Wood-Mason).

In contrast with the Australian fauna, the New Zealand stomatopod fauna, although impoverished, is very poorly known. Eight species have been recorded from New Zealand, but the occurrences of only three, *Squilla armata* H. Milne-Edwards, *Heterosquilla tricarinata* (Claus), and *H. brazieri* (Miers), have been verified. These three species have been treated in the present paper.

The status of the following five species recorded from New Zealand is not clear: *Squilla nepa:* Heller, 1865; *S. armata:* Kirk, 1879 (part); *S. affinis:* Chilton, 1891, 1911; *S. tridentata* Thomson, 1882; and *Protosquilla trispinosa*: Heller, 1865. No attempt will be made here to comment on these records. A future paper is planned with J. C. Yaldwyn to treat the New Zealand fauna as a whole and to give new records for that area.

Available collections of stomatopods from New Zealand should be studied in the light of current knowledge in order to determine the status of the five species mentioned above and to give a firmer basis for assessing the relationships of the New

Zealand fauna. It seems probable that numerous specimens of stomatopods have been collected since the New Zealand species were last studied by Chilton (1911). Also, a comparative study of series of *S. armata* from New Zealand, South Africa, and South America should be made. As pointed out below, it is not unlikely that the New Zealand *S. armata* is a distinct population or a distinct species.

Only four published references to stomatopods collected by the *Endeavour* are known. *Hemisquilla ensigera* (Owen) was reported by Stephenson (1953, 1955) and Stephenson and McNeill (1955), and *Squilla inornata* Tate was recorded by Stephenson (1953). As Stephenson has studied most stomatopod collections present in Australian museums it is likely that the *Endeavour* specimens discussed herein form the remainder of that collection.

METHODS

Synonymies, unless prefixed by the phrase "Restricted Synonymy", are as complete as possible; in general, there is little need to provide complete synonymies for these have been given recently by Stephenson and McNeill (1955). The synonymies usually include references to the original description, the papers by Kemp (1913), Holthuis (1941), together with references to pertinent papers published since 1941. Generic synonymies are brief, and, for the more recently recognized genera, the citation of the original publication is given. For older genera no citation is needed.

The bibliography includes all references cited herein as well as all papers dealing with adult stomatopods from the Indo-Pacific published since 1941 that have come to my attention. The present bibliography, in combination with those given by Kemp (1913), Balss (1938), and Holthuis (1941), should provide almost complete coverage of the Indo-Pacific stomatopods.

Measurements used herein are given in mm. In the material examined, the numerals following the number of specimens denote total length (TL), unless carapace length (CL) is specified; the latter is given only for broken or damaged specimens. Total length is measured along the midline from the apex of the rostral plate to the apices of the submedian teeth of the telson; carapace length is also measured along the midline and does not include the rostral plate. The width of the abdomen is always measured at the fifth somite; this is usually the widest portion of the abdomen and a measurement here, immediately anterior to the uropods, eliminates the necessity of counting somites to make sure the same one is always measured. Broken specimens are indicated by the abbreviation "brk.".

An abdominal spine formula of: submedian, 6; intermediate, (1) 2-6; lateral, 2-6; marginal, 1-5, indicates that the submedian carinae terminate in spines on the sixth somite only, the intermediates and laterals are spined on the second to sixth somites, inclusive, and the marginal carinae are armed on the first five somites. The parenthesis in the formula indicates that on that somite the carina may be armed. A telson denticle formula of "5, 7-10, 1" indicates that on the telson margin there are 5 submedian, 7-10 intermediate, and 1 marginal denticle. The count of teeth on the dactylus of the raptorial claw always includes the terminal tooth.

Several indices are used below, and all are based on the relative length of a specific portion of the body to the carapace length, × 100. A much more reliable index can be calculated from the carapace length than from the total length, which is highly variable and difficult to measure accurately; total length is used here only to give an indication of the overall size of the specimens. The Corneal Index (CI) is

calculated as Carapace Length/Cornea Width × 100; this is comparable to Kemp's Corneal Index, which was only a ratio. In *Gonodactylus* the Abdominal Width/Carapace Length Index (AWCLI) is used as an expression of the relative width of the body.

The following abbreviations are used to show the disposition of the material reported herein: AM (Australian Museum); BM(NH) (British Museum (Natural History)); MNHNP (Muséum National d'Histoire Naturelle, Paris); MCZ (Museum of Comparative Zoology, Harvard); RNHL (Rijksmuseum van Natuurlijke Historie, Leiden); USNM (U.S. National Museum). As part of the original agreement between the Australian Museum and the U.S. National Museum, types and one-half of the material collected by the Arnhem Land Expedition are to be deposited in the Australian Museum.

ACKNOWLEDGEMENTS

Many people have contributed to this study. J. C. Yaldwyn, of the Australian Museum, provided encouragement for working up the *Endeavour* collection, allowed a great deal of latitude in the expansion of the report, and supplied many critical specimens on loan and exchange, including a paratype of *Manningia notialis*. W. Stephenson, University of Queensland, commented upon some of the problems treated here and was instrumental in obtaining a specimen of *Manningia* from the Queensland Museum, through the late George Mack, then its Director. J. Forest made available on loan a specimen of *H. tricarinata* from the collection of the Muséum National d'Histoire Naturelle, Paris. L. R. Richardson, Victoria University of Wellington, donated three specimens of *S. armata* from New Zealand. On a recent trip to Europe, made possible by a grant from the National Science Foundation (NSF GB-1602), I had the opportunity of examining stomatopods in several museums. At the British Museum, Angela Evans and R. W. Ingle spent a great deal of time helping me locate specimens and literature; Ingle also expedited the loan of several specimens. At the Rijksmuseum van Natuurlijke Historie at Leiden, L. B. Holthuis spent the greater part of a week helping me locate specimens, especially de Haan's types. With the help of J. Stock at the Zoological Museum, Amsterdam, I was able to examine the important Siboga collection of stomatopods. The illustrations provided herein were executed by my wife, Lilly, under National Science Foundation Grant GB-1602; NSF support of studies on stomatopod systematics is gratefully acknowledged. Several of my colleagues, including F. A. Chace, Jr, D. L. Pawson, and H. H. Hobbs, Jr, provided helpful criticism of various portions of the manuscript.

SYSTEMATIC ACCOUNT

KEY TO GENERA OF STOMATOPOD CRUSTACEANS KNOWN FROM AUSTRALIA

1. Telson with well-defined median dorsal carina 2
   Dorsal surface of telson smooth or with a broad, raised area, but without a sharp median carina 11

2. Four or more intermediate denticles present on posterior margin of telson 3
   No more than two intermediate denticles on posterior margin of telson 5

3. Eyes small, cornea not as broad as dilated stalk; eye-scales fused; carapace usually with few carinae ..... *Clorida*, p. 86
   Eyes large or small, cornea as broad as or broader than stalk (except *Squilla foveolata*); eye-scales separate; carapace usually with normal complement of carinae 4

4. Posterolateral margin of carapace with deep excavation posterior to angular lobe; propodus of raptorial claw with erect spines on upper margin ..... *Harpiosquilla*, p. 87
Posterolateral margin of carapace not deeply excavated; propodus of claw with even pectinations on upper margin ..... *Squilla*, p. 89

5. Ischiomeral articulation of raptorial claw terminal 6
Ischiomeral articulation of raptorial claw distal to proximal end of merus 8

6. Dactylus of raptorial claw unarmed; rostral plate triangular; telson with three longitudinal carinae ..... *Hemisquilla*, p. 102
Dactylus of claw with teeth on inner margin; rostral plate variously shaped, not triangular; telson with more than three longitudinal carinae 7

7. Dactylus of claw with three teeth; rostral plate ovate; basal prolongation of uropod with two spines, outer longer, inner without spinules [*Pseudosquilla*]
Dactylus of claw with four teeth; rostral plate pentagonal; basal prolongation of uropod with two spines, inner longer, with spinules on inner margin ..... *Manningia*, p. 102

8. Dactylus of claw armed on inner margin; rostral plate unarmed *Odontodactylus*, p. 105
Dactylus of claw unarmed; rostral plate with at least one sharp spine 9

9. Anterolateral angles of carapace not in advance of base of rostral plate; posterior margin of sixth abdominal somite concave .... *Protosquilla*, p. 106
Anterolateral angles of carapace in advance of rostral plate; posterior margin of sixth abdominal somite straight or slightly convex 10

10. Rostral plate sharply trispinous ..... [*Mesacturus*]
Rostral plate with sharp median spine, anterolateral angles rounded or acute but not produced into spines ..... *Gonodactylus*, p. 107

11. Dorsal surface of telson without spines or prominent, raised median projection, marginal teeth and denticles largely fused..... [*Lysiosquilla*]
Dorsal surface of telson with transverse row of spines or prominent median projection, marginal teeth and denticles distinct 12

12. Dorsal armature of telson consisting of a semicircular, transverse row of 5 or more spines, median spine neither carinate nor on a broad median projection ..... [*Acanthosquilla*]
Telson with broad, raised median area, lateral spines or carinae present or absent 13

13. Median projection of telson broad, truncate; posterior margin of telson with four pairs of lateral projections, not carinate anteriorly, above marginal armature ..... *Hadrosquilla*, p. 115
Median projection of telson broad or tapering, apex sharp or obtuse, not truncate; lateral projections of telson, if present, carinate anteriorly ..... *Heterosquilla*, p. 118

Clorida Eydoux and Souleyet, 1842

Clorida Eydoux and Souleyet, 1842, p. 264.

Remarks.—In his discussion of the relationship of *Squilla granti*, Stephenson (1953a) pointed out that the "*Chloridella*" group of *Squilla*, to which *S. granti* belongs, does not conform to Kemp's (1913) widely accepted definition of the genus. This "group" corresponds to the genus *Clorida* which may be characterized by the following combination of characters: (1) the eyes are small, with the stalks dilated, broader than the cornea; (2) the eye-scales are fused; (3) the carinae of the carapace are poorly developed, generally being present on the posterior portion only; (4) the ischiomeral articulation of the raptorial claw is not really terminal, but is situated to one side of the proximal end of the merus; and (5) the submedian marginal teeth of the telson have movable apices.

Clorida now includes 11 species: *Squilla microphthalma* H. Milne-Edwards, 1837; *Clorida latreillei* Eydoux and Souleyet, 1842; *Clorida decorata* Wood-Mason, 1875; *Chloridella depressa* Miers, 1880; *Chloridella rotundicauda* Miers, 1880; *Squilla chlorida* Brooks, 1886; *Squilla gibba* Nobili, 1903; *Squilla verrucosa* Hansen, 1926; *Squilla choprai* Tweedie, 1935; *Squilla merguiensis* Tiwari and Biswas, 1952; and *Squilla granti* Stephenson, 1953. *Squilla fallax* Bouvier, 1914, may also belong in this genus. Of these, only three species, *C. depressa*, *C. microphthalma*, and *C. granti* have been recorded from Australia. Comments on the nomenclature of *Clorida* are included in a paper on stomatopods for the *Treatise on Invertebrate Paleontology* (Holthuis and Manning, in press).

During a recent visit to the British Museum (Natural History) I had the opportunity of examining the type of *C. depressa* as well as a specimen of *C. microphthalma* from Australia. Notes on both of these are given below.

Clorida depressa (Miers, 1880)

Restricted synonymy:—

Chloridella microphthalma: Miers, 1880, p. 14, pl. II, figs 1-4 [provisionally named *C. depressa* on p. 15] [not *S. microphthalma* H. Milne-Edwards, 1837].

Squilla depressa: Serène, 1952, p. 2, text-figs 3-4, 9, 18, 21, pl. 1, figs 3, 6, pl. 2, figs 3, 6-10—Stephenson and McNeill, 1955, p. 240 [and synonymy].

Material.—1♂, 37.0; Port Essington, Northern Territory; holotype; BM(NH) Reg. No. 1957.12.21.1.

Diagnosis.—Eyes small, not extending past midpoint of basal segment of antennular peduncle; cornea small, not half as long as eye but about half as wide as stalk; eyes not divergent, inner margins appressed for at least half their length; eye-scales fused, feebly indented along midline; antennular peduncle shorter than carapace; rostral plate semicircular; 4 epipods present; mandibular palp present; merus of raptorial claw extending to cornea; abdominal carinae spined as follows: submedian, 6; intermediate, 5-6; lateral, 5-6; marginal, 1-5.

Discussion.—*C. depressa* was provisionally synonymized with *C. microphthalma* by Kemp (1913) and only recently has been redescribed by Serène (1952), who pointed out the differences between the two species. The type agrees with Serène's account in most details, differing only in that the eyes are appressed for at least half their length rather than being divergent from their bases.

The presence of a mandibular palp distinguishes this species from *C. granti* and the short eyes, semicircular rostral plate, and larger number of spined marginal abdominal carinae distinguishes it from *C. microphthalma*.

Distribution.—Known only from Australia, where it has been recorded from the Northern Territory and several localities in Queensland. Shallow water.

Clorida microphthalma (H. Milne-Edwards, 1837)

Restricted synonymy:—

Squilla microphthalma: H. Milne-Edwards, 1837, p. 523—Kemp, 1913, p. 31, pl. I, figs 17-20—Stephenson, 1962, p. 39, pl. I, figs E, F, G, text-fig. 2.

Material.—1♂, 43.3; Roebuck Bay, Western Australia; Mrs B. Gray; BM(NH) Reg. No. 1932.11.30.191.

Remarks.—This specimen agrees well with Stephenson's (1962) account of specimens from the same locality, differing only in that the rostral plate is triangular and one of the marginal carinae of the third abdominal somite is armed posteriorly on one side.

Distribution.—Western Indo-Pacific, from Indonesia, Viet Nam and Australia to India and Zanzibar. In Australia it has been recorded from Western Australia and the Northern Territory. Littoral to 60 m.

Harpiosquilla Holthuis, 1964

Harpiosquilla Holthuis, 1964, p. 140.

Remarks.—This genus was erected to include three species heretofore placed in *Squilla*, *S. raphidea* Fabricius, 1798, *S. harpax* de Haan, 1844, and *S. annandalei* Kemp, 1911. *H. harpax* had been considered a synonym of *H. raphidea* until recently, when Tiwari and Biswas (1952) showed that they were distinct.

One of the specimens sent to the U.S. National Museum on exchange from the Australian Museum by J. C. Yaldwyn is apparently *H. harpax*. It seems likely that other specimens from Australia among those reported by Stephenson and McNeill (1955) as *Squilla raphidea* will also prove to be *H. harpax*. Judging by the size range reported by those authors for their material (TL 132-314 mm), both species are present in Australia.

The specimen described below differs from the account of *H. harpax* given by Tiwari and Biswas in several respects, and it also differs from specimens from other localities available for comparison. The entire *Harpiosquilla* complex needs to be re-examined to determine whether or not one or more undescribed species, related to *H. harpax*, exist or to determine the variability of that species. Particular attention should be paid to the abdominal carination, the shape of the lobe on the inner spine of the basal prolongation of the uropod, and the colour pattern.

Harpiosquilla harpax (de Haan, 1844)

Fig. 1

Squilla harpax de Haan, 1844, atlas, pl. li, fig. 1—Tiwari and Biswas, 1952, p. 358, text-fig. 3b, d, f—Ingle, 1963, p. 18, figs 9, 59.

Harpiosquilla harpax: Holthuis, 1964, p. 140 [discussion].

Material.—1♀, 170.0; Darwin, Northern Territory; early 1954; Capt. F. E. Wells, Harbourmaster, col.; exchange from Australian Museum, USNM 111354.

Diagnosis.—Antennular peduncle shorter than carapace; eye large, CI 336; lateral margins of rostral plate faintly sinuous, not markedly concave distally, apex short; carapace narrowed anteriorly, anterior width less than one-half median

length; carinae of carapace discernible, not sharply developed; dactylus of raptorial claw with 7 teeth; mandibular palp and 5 epipods present; lateral process of fifth thoracic somite unarmed; intermediate carinae of thoracic somites unarmed posteriorly; ventral keel of eighth thoracic somite broadly rounded, inclined posteriorly; submedian carinae of abdomen present; abdominal carinae spined as follows: submedian, 6; intermediate, 2-6; lateral, 1-6; marginal, 1-5; sixth abdominal somite with median keel on posterior half of ventral surface; telson as broad as long, denticles sharp, 5, 7-10, 1; prelateral lobe present dorsally, carina of lateral tooth over two-thirds as long as carina of prelateral lobe; lobe on outer margin of inner spine of basal prolongation of uropod with margin straight or convex, not strongly concave.

Fig. 1.—*Harpiosquilla harpax* (de Haan), female, TL 170.0 mm, Darwin. Lateral processes of thoracic somites and posterior portion of carapace.

Colour.—Dark pigment at least partially faded in this specimen, except for single dark spot on upper distal portion of merus of raptorial claw, dark lines on carinae and grooves of carapace and on posterior margins of all somites except for sixth abdominal; telson with elongate black patch, fully half as long as telson, on each side of median crest; uropods with faint indications of pigment.

Measurements.—Female, TL 170.0; carapace length, 30.6; anterior width of carapace, 13.6; cornea width, 9.1; rostral plate length, width, 5.7, 5.1; telson length, width, 29.0, 29.0.

Discussion.—This specimen differs from those reported by Tiwari and Biswas (1952) and from others in the collection of the U.S. National Museum in the following features: (1) the cornea is less broad (CI 336 instead of 270-320) and is noticeably stouter; (2) the carapace is narrower anteriorly and the carinae are not as sharply defined; (3) the submedian carinae of the abdomen are well-developed; (4) the telson is shaped and ornamented differently; it is as broad as long, the denticles are sharp, not rounded, and the prelateral lobe is well-formed dorsally; in addition, the carina of the prelateral lobe is noticeably shorter; (5) the lobe on the inner spine of the basal prolongation of the uropod is not strongly concave but is almost convex; and (6) there is one pair of elongate rectangular black pigment spots on the telson rather than a pair of small black squares.

These differences strongly suggest that there is more than one species involved in the currently-recognized *H. harpax* but it is not possible to determine whether or not the Australian form is *harpax* without comparing it directly with type material. The Australian form more nearly resembles de Haan's illustration of *H. harpax*, for he shows the carinate abdomen and the straight lobe on the basal prolongation of the uropod, than the specimens described by Tiwari and Biswas (1952).

The possibility that *H. harpax* is variable in the features mentioned above cannot be overlooked. A large series of specimens from different localities must be studied before the problem can be solved.

Distribution.—Indo-Pacific, from Japan and northern Australia westward to the Red Sea (Tiwari and Biswas, 1952; Ingle, 1963). Depth range unknown.

Squilla Fabricius, 1787

Remarks.—*Squilla*, which now includes over eighty species, is not only one of the largest but also is one of the best known of the stomatopod genera. With few exceptions the Indo-Pacific species, at least, have been reasonably characterized and illustrated, largely due to the efforts of Kemp (1913). It was somewhat surprising, then, to learn from a comparison of types that *S. oratoria* var. *perpensa* Kemp, 1911, was conspecific with *S. anomala* Tweedie, 1935, and distinct from *S. inornata* Tate, 1883. Kemp's species had been synonymized with Tate's and was considered to be distinct from *S. anomala*. Although the Indo-Pacific species of *Squilla* are comparatively well known, little is known about geographic variation or the overall range of many species. Thus it is still worthwhile to provide diagnoses and figures of material at hand when collections from limited geographic areas or areas beyond the known range of species are reported. For this reason diagnoses and sketches of diagnostic features, based on Australian specimens, are presented here for three members of the *S. oratoria* complex (*S. inornata*, *S. interrupta*, and *S. woodmasoni*).

Perhaps it will also be of value to comment here on the status of varietal forms such as those recognized by Kemp (1913) and some subsequent workers. Kemp used variety to indicate close affinity and/or similarity, as in *Gonodactylus chiragra* var. *platysoma*, *Lysiosquilla maculata* var. *sulcirostris*, and *Squilla oratoria* var. *perpensa*, among others. These varieties differed from the "typical" species in seemingly minor details, but the differences were constant. Although these "forms" were called varieties by Kemp and subsequent workers, they were treated as species. The term variety was not necessarily used to indicate a geographic race (subspecies) or an unnamable variant. In some cases Kemp's varieties were sympatric (*chiragra* and *platysoma*), in others they were allopatric (*oratoria* and *perpensa*). All three of the examples

mentioned above are valid, recognizable species in my opinion. They are distinct throughout their ranges and there is no evidence of intergradation where they are found together.

Sixteen species of *Squilla*, not including the species currently placed in *Clorida* and *Harpiosquilla*, have been recorded from Australia, and six of these are reported here. Among the Australian species are five members of the *S. oratoria* complex. Since there has been considerable confusion in the past over the diagnostic features of these similar but distinct species, a table is included summarizing these features for the Australian species.

A description of the single species of *Squilla*, *S. armata* H. Milne-Edwards, known with certainty to occur in New Zealand, is also included. *S. armata* and its ally *S. gracilipes* Miers share one feature which distinguishes them from all other species of *Squilla*, eye-scales produced into strong, anteriorly-directed spines. This feature, in combination with the reduction of carinae on the carapace, loss of the prelateral lobe and the presence of movable apices on the submedian teeth of the telson, and the restriction of these species to cold temperate waters of the Southern Hemisphere, seem to indicate separation at the generic level. The name *Pterygosquilla* Hilgendorf, proposed in 1890 for *P. laticauda* (a synonym of *Squilla gracilipes*), is available. Additional work with a larger series of specimens of *S. armata* and further analysis of characters within *Squilla* might well show that *Pterygosquilla* should be recognized.

Squilla armata H. Milne-Edwards, 1837

Fig. 2

Restricted synonymy:—

Squilla armata H. Milne-Edwards, 1837, p. 251.—Hector, 1877, p. 474.—Kirk, 1879a, p. 401.—Miers, 1880, p. 26.—Filhol, 1885, p. 52 [listed]; 1886, p. 435 [listed]. —Chilton, 1891, p. 60.—Hutton, 1904, p. 256 [listed].—Chilton, 1911, p. 135, text-figs 1-2; 1911a, p. 306.—Kemp, 1913, p. 41, pl. II, figs 28-29.—Thomson, 1913, p. 241.—Thomson and Anderton, 1921, p. 108.—Parisi, 1922, p. 93.

not *Squilla armata:* Whitelegge, 1900, p. 199 [=*S. mcneilli* Stephenson].

Squilla armata var. *schizodontia* Richardson, 1953, p. 315, text-figs 1-3.

Material.—2♂, 113.6-114.3; 1♀, 121.7; New Zealand; no other data; from L. R. Richardson; USNM 112415.—1♀, 118.2; Laurie Harbor, Auckland Is.; BM(NH) Reg. No. 45.69.

Diagnosis.—Body rough, covered with minute tubercles; antennular peduncle slightly shorter than carapace; eyes of moderate size, set obliquely on stalk, CI 481-521; eye-scales produced into erect spinules; anterior margin of ophthalmic somite projecting forward, bituberculate; rostral plate triangular, lateral margins sinuous, apex rounded; carapace without median carina, other carinae reduced, reflected marginals and short laterals only present, laterals extending just anterior to cervical groove; dactylus of raptorial claw with 6-8 teeth, outer margin flattened but not markedly sinuate; dorsal ridge of carpus undivided, terminating in strong tooth; merus unarmed inferodistally; mandibular palp absent; 4 epipods present; lateral process of fifth thoracic somite a sharp spine directed laterally, ventral spines of fifth somite absent or reduced to blunt lobes; lateral processes of sixth and seventh thoracic somites rounded laterally, spined posteriorly; distance between submedian abdominal carinae about one-third distance between intermediates, submedian carinae very distinct; abdominal carinae spined as follows: submedian, 6; intermediate, (2-3) 4-6; lateral, (2) 3-6; marginal, 1-5; fifth somite with 2-5 accessory spinules on each side lateral to submedian carinae; telson with 3 pairs of marginal teeth, submedians with movable apices,

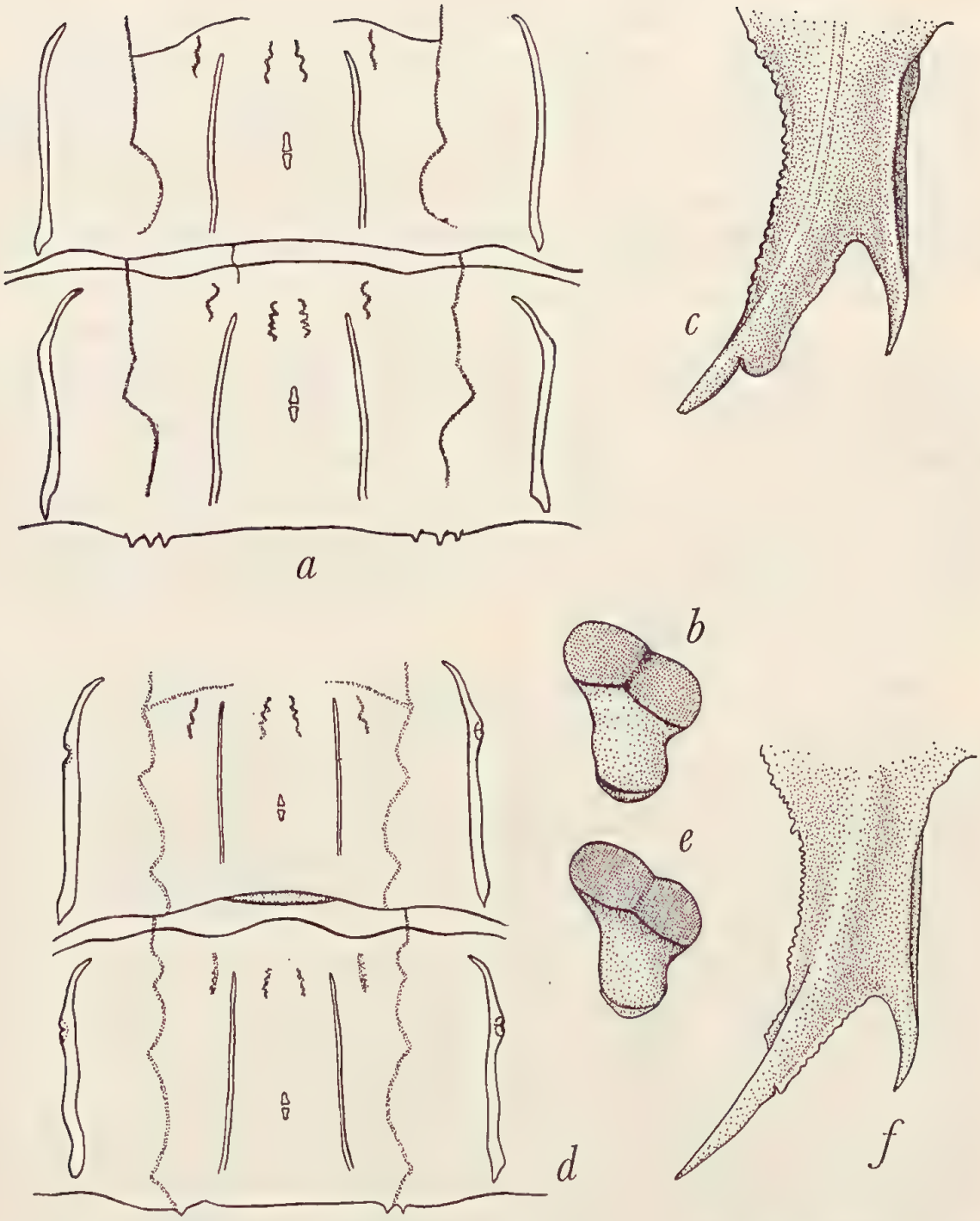

Fig. 2.—*Squilla armata* H. Milne-Edwards, male, TL 114.3 mm, New Zealand: *a*, fourth and fifth abdominal somites, dorsal view; *b*, eye; *c*, basal prolongation of uropod. Male, TL 109.7 mm, Chile: *d*, fourth and fifth abdominal somites, dorsal view; *e*, eye; *f*, basal prolongation of uropod.

prelateral lobes absent; denticles 1, 7-9, 1; telson with submedian tubercle on each side of anterior surface; ventral surface of telson with postanal keel; uropod with 7-8 movable spines, last short, on outer margin of penultimate segment of outer branch; basal prolongation of uropod with broad, rounded lobe on outer margin of inner spine.

Colour.—Completely faded in the present material and not recorded in the literature. A photograph of a living specimen was published in the New Zealand journal, *Tuatara* (Anonymous, 1964).

Size.—Males, TL 113.6-114.3 mm; females, TL 118.2-121.7 mm.

Discussion.—Richardson (1953) has suggested that the New Zealand population of *S. armata*, which he provisionally named *S. armata* var. *schizodontia*, might prove to be distinct from populations occurring off South Africa and South America. His suggestion was based upon the following features which he observed on New Zealand specimens: (1) more teeth on the dactylus of the raptorial claw; (2) wider range in number of accessory spinules on the fifth abdominal somite; (3) subdivision of the intermediate marginal denticles of the telson. These features are found in combination with a tendency towards subdivision or splitting of spines. Unfortunately, Richardson had no comparative material from other areas; the apparent differences reported by him were based upon comparisons of his observations with accounts in the literature.

Direct comparison of material from Chile with specimens from New Zealand seems to substantiate Richardson's statement as to the distinctness of the populations, but for different reasons. There is a great deal of overlap between Chilean and New Zealand specimens in the features mentioned by Richardson, as follows: (1) he noted that there were 6-8 teeth on the dactylus of the raptorial claw; Chilean specimens have 6-9; (2) New Zealand specimens had 1-5 accessory spinules on each side of the fifth abdominal somite, 2-10 total; the Chilean specimens have 0-4 on each side, 0-7 total; (3) there were 7-11 intermediate denticles on the telson of Richardson's New Zealand specimens; there are 7-13 in the Chilean. Some bifurcation of teeth is present in the Chilean specimens but not to the same extent as reported for New Zealand specimens by Richardson.

There are other differences in specimens from the two areas which in my opinion are of greater importance and which support the idea of distinct populations; these include: (1) the submedian carinae of the first five abdominal somites are more distinct and appear to be wider apart (one-third the distance between the intermediate carinae) (fig. 2a) on the New Zealand specimens than on those from Chile (one-fourth the distance between the intermediates) (fig. 2d); (2) the lobe on the outer margin of the inner spine of the basal prolongation of the uropod is much larger in the New Zealand specimens than in those from Chile (compare figs 2c and 2f). In addition to these two features, which seem to show the most important distinctions between specimens from the two areas, the abdominal carinae are much more distinct in the few specimens; (3) from New Zealand available for comparison with specimens from Chile, and there are slight differences in the shape of the eyes (figs 2b and 2e).

Although no specimens from South Africa are available at the time of this writing, I have been able to examine three specimens from that area through the courtesy of the South Africa Museum. These specimens differ from those from the other two areas in having very faint abdominal carinae, in lacking the accessory spinules on the fifth abdominal somite, and in having the two lobes of the cornea more pronounced. The lobe on the basal prolongation of the uropod is intermediate in size and shape between lobes on specimens from the other two areas. Also, the South African material examined by me had only the intermediate and lateral carinae of the last three abdominal somites armed with spinules; this feature might be expected to vary with a larger sample.

In view of the small size of the samples from the three areas and the immediate lack of specimens from South Africa, it seems best not to recognize a subspecies from New Zealand at this time. Further study with series of specimens from each area would probably indicate that three subspecies or species could be recognized.

S. armata is closely related to *S. gracilipes* Miers from Patagonia; both species differ from all others in the genus in having eye-scales produced into strong spines. In view of the shape of the eye-scales and other differences between these two species and the other members of *Squilla*, it seems likely that *Pterygosquilla*, which was erected

by Hilgendorf (1890) for *P. laticauda* (a junior synonym of *S. gracilipes*), should be separated from *Squilla*; further study will be required before this can be done.

Remarks.—The diagnosis given above is based entirely on the three specimens from New Zealand in the U.S. National Museum; all other descriptions appear to be based either on specimens from more than one area, on other accounts in the literature, or on American specimens only.

Although Bigelow (1894) noted that sexual dimorphism was not evident in his material from Patagonia, the present specimens from New Zealand are noticeably dimorphic. In males, the bases of the marginal teeth of the telson and the abdominal pleura between the lateral and marginal carinae are noticeably swollen.

Distribution.—*S. armata* is a southern cold-temperate or subantarctic species, known from South America, New Zealand, and South Africa. In New Zealand it has been recorded from Petone Beach, Wellington Harbour; Cook Strait; Dunedin, Otago; and Laurie Harbor, Auckland Is. The bathymetric range in New Zealand has not been recorded, but in other areas it has been collected in depths to 222 m.

In the legend of the photograph published in *Tuatara* (Anonymous, 1964), *S. armata* is said to occur in southern Australia. To my knowledge, the species does not occur there. Possibly Whitelegge's (1900) reference to *S. armata* was used as a source of information. As Stephenson (1953a) pointed out, *S. armata*: Whitelegge is actually *S. mcneilli* Stephenson, 1953.

Squilla foveolata Wood-Mason, 1895

Squilla foveolata Wood-Mason, 1895, p. 2, pl. 2, fig. 1.—Kemp, 1913, p. 58, pl. IV, fig. 48.—Kemp and Chopra, 1921, p. 29 [listed].—Liu, 1949, p. 30, pl. IV, figs 4, 5.—Stephenson, 1953, p. 41.—Stephenson and McNeill, 1955, p. 243 [listed].

Chloridella foveolata:Schmitt, 1929, p. 133, pl. 16, figs 1, 2.

Material.—1♂, 58.0; 12 mi. NNE of Bowen, Queensland; 35-46 m; *Endeavour*; AM Reg. No. P. 3530.

Discussion.—This specimen agrees well with Kemp's account in almost all respects, but the following minor differences were noted: (1) the anterior margin of the ophthalmic somite is not rectangular but rounded; (2) there is a prominent, posteriorly-directed spine on the basal segment of the raptorial claw; (3) the anterior portion of the bifurcated lateral process on the fifth thoracic somite is a sharp spine, directed anteriorly, but the upper, posterior lobe is spatulate, with the apex rounded; (4) the abdominal carinae are spined as follows: submedian, 4-6; intermediate, 4-6; lateral, 3-6; marginal, 1-5; in Kemp's material the submedian and intermediate carinae of the third were armed in some specimens. These differences are minor and fall within the expected variation for this species.

Remarks.—The body carinae are almost all ornamented with one or two parallel lines of pits which form what Kemp described as a meshlike reticulation; the carinae are defined by the reticulations rather than being obscured by them.

The eyes of *S. foveolata* resemble those found in some species of *Clorida;* the stalk is noticeably expanded. In all other respects *S. foveolata* agrees with *Squilla.*

Distribution.—This species has been reported from China, Burma, and Queensland, Australia; Stephenson (1953) recorded it from the latter locality. Shallow water to moderate depths, 5-84 m.

Table 1

Comparison of the major diagnostic features of five species of the *Squilla oratoria* complex from Australia (data partially from Kemp, 1913)

	S. inornata Tate, 1883	*S. perpensa* Kemp, 1911	*S. fabricii* Holthuis, 1941	*S. interrupta* Kemp, 1911	*S. woodmasoni* Kemp, 1911
Rostral Plate	Longer than broad	Broader than long	Broader than long	Broader than long	Broader than long
Anterior Width of Carapace ..	Less than 1/2 CL plus rostral plate.	Less than 1/2 CL plus rostral plate.	Less than 1/2 CL plus rostral plate.	Less than 1/2 CL plus rostral plate.	More than 1/2 CL plus rostral plate.
Median Carina of Carapace ..	Interrupted at bifurcation.	Interrupted at bifurcation.	Interrupted at bifurcation.	Interrupted at bifurcation.	Bifurcation obsolete.
Corneal Index	352-424	397-468	323-429	500-610	300-420
Dorsal Ridge of Carpus of Claw	Undivided ..	Undivided ..	Irregularly tuberculate.	2 tubercles ..	2-3 tubercles
Spine Formula, Abdomen ..	5-6; 4-6; 2-6; 1-5	5-6; 4-6; 3-6; 1-5	4-6; 3-6; 1-6; 1-5	5-6; 4-6; 3-6; 1-5	5-6; 3-6; 2-6; 1-5
Margin of Lobe on Basal Prolongation of Uropod.	Concave	Concave	Concave	Convex	Concave

Squilla inornata Tate, 1883

Fig. 3

Restricted synonymy:—

Squilla inornata Tate, 1883, p. 51, pl. ii, figs 3a-c.

Squilla oratoria var. *perpensa:* Kemp, 1913, p. 70 [part; not *S. oratoria* var. *perpensa* Kemp, 1911, =*S. anomala* Tweedie, 1935].—Hansen, 1926, p. 11.

Squilla oratoria var. *inornata:* Hale, 1924, p. 495; 1927, p. 32, fig. 22.—Chopra, 1934, p. 25 [part].—Tweedie, 1935, p. 48 [discussion].—Holthuis, 1941, p. 248.

Material.—1♂, 72.5; 1♀, 89.5; 12 mi. NNE of Bowen, Queensland; 35-46 m; *Endeavour*; AM Reg. No. P. 3530.—1♂, 90.8; same; USNM 111379.

In addition to these specimens from the *Endeavour* collection, I have examined these specimens reported from several Indo-Malayan localities by Holthuis (1941), the Siboga specimens reported by Hansen (1926), and that from Singapore in the British Museum reported by Kemp (1913). All are conspecific with the species reported here.

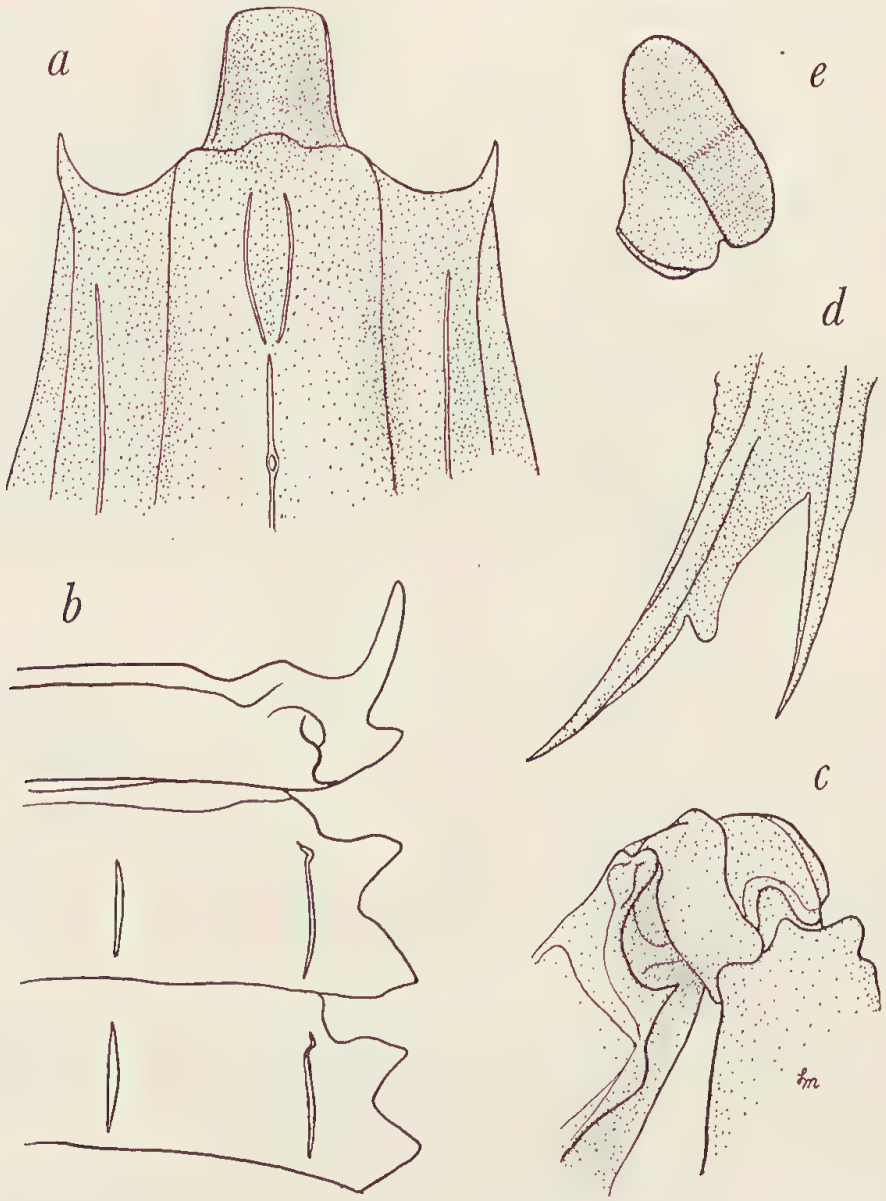

Fig. 3.—*Squilla inornata* Tate, male, TL 72.5 mm, off Bowen. *a*, anterior portion of carapace and rostral plate; *b*, lateral processes of fifth, sixth, and seventh thoracic somites; *c*, carpus of raptorial claw; *d*, basal prolongation of uropod; *e*, eye.

Diagnosis.—Antennular peduncle not as long as carapace; eyes large, set obliquely on stalk, CI 414-424 in *Endeavour* specimens; anterior margin of ophthalmic somite projecting forward, truncate or emarginate along midline; rostral plate elongate, longer than broad, apex usually truncate; median carina of carapace usually interrupted at base of bifurcation, distance from dorsal pit to bifurcation less than distance from bifurcation to anterior margin; intermediate carinae of carapace convergent anteriorly with laterals; dactylus of raptorial claw with 6 teeth, outer margin sinuate; dorsal ridge of carpus undivided; merus with blunt inferodistal spine; mandibular palp and 4 epipods present; lateral process of fifth thoracic somite with sharp anterior spine and short, angular posterior lobe; lateral process of sixth thoracic somite bilobed, anterior lobe large but smaller than posterior, truncate, posterior lobe triangular, apex not sharp; lateral process of seventh thoracic somite bilobed, anterior lobe triangular, smaller and sharper than posterior which is almost cordiform; abdominal carinae spined as follows: submedian, 5-6; intermediate, 4-6; lateral, 2-6; marginal, 1-5; telson with 3-4, 7-8, 1 rounded denticles; lobe on outer margin of inner spine of basal prolongation of uropod rounded, projecting, inner margin concave.

Colour.—Completely faded in the *Endeavour* specimens. Specimens from other localities have each of the body segments outlined posteriorly in dark pigment, the carinae of the marginal teeth of the telson dark, and a dark spot on the uropod, with the black pigment on the inner half of the distal segment sharply separated from the clear inner half, and the distal half of the inner branch of the uropod dark on both sides, lighter along the midline.

Size.—Males, TL 72.5-90.8 mm; only female, TL 89.5 mm.

Discussion.—The close similarity between *Squilla perpensa* Kemp, 1911 and *Squilla inornata* Tate, 1883 led Chopra (1934), who directly compared type-specimens, to consider them to be conspecific; in this Chopra followed Hale (1924). Apparently Tate's paper had been overlooked by Kemp, for *S. inornata* was not mentioned in any of Kemp's accounts. Unfortunately, Kemp (1911, 1913) did not provide a full description of *S. perpensa*, but merely pointed out the most obvious differences between it and the other members of the *S. oratoria* complex, namely, the presence of an undivided ridge on the carpus of the raptorial claw. In 1913 Kemp did provide illustrations of *perpensa*, and he showed a form with small eyes and a short, broad rostral plate.

In indicating that *inornata* Tate was identical with *perpensa* Kemp, Chopra (*loc. cit.*) noted that the Australian specimen differs from those from India in two features, (1) the rostral plate is longer and slenderer, and (2) the anterior lobe of the lateral process of the sixth thoracic somite is bluntly pointed. These are important observations, for the two characters mentioned can be used to distinguish *S. inornata* from *S. perpensa*; Tate (1885) also remarked on the long rostral plate of his specimens.

The problem was further complicated by the description in 1935 of *Squilla anomala* Tweedie, from Singapore. Tweedie pointed out that the eyes of *S. anomala* are small and the rostral plate is short, and gave other differences between his species and *S. interrupta* and *S. inornata* (as *S. oratoria inornata*).

A comparison of Tweedie's types with specimens of *S. perpensa*, including types, identified by Kemp in the collection of the British Museum, showed that *S. anomala* is a junior synonym of *S. perpensa*. *S. perpensa* is the older name.

The specimen from Singapore in the collection of the British Museum reported by Kemp (1913, p. 72) as *S. oratoria* var. *perpensa* is *S. inornata*. All of the other specimens in the British Museum collection reported by Kemp under the varietal name are clearly referable to *S. perpensa*.

S. inornata differs from *S. perpensa* in the following features: (1) the eye of *inornata* is larger, with the Corneal Index ranging from 352-424, larger in smaller specimens; the Corneal Index for *perpensa* ranges from 397-468. Although there is some overlap in this index, specimens of *inornata* when compared with specimens of *S. perpensa* of similar size always have a larger eye, and, of course, a smaller Corneal Index; the indices for the largest specimens of *inornata* are similar to those for small specimens of *perpensa*; (2) the rostral plate of *inornata* is slender, longer than broad; in *perpensa* it is short, blunt, broader than long; (3) the anterior lobe of the lateral process of the sixth thoracic somite is more truncate in *inornata* than in *perpensa*; (4) the lateral carina of the second abdominal somite is usually armed posteriorly in *inornata*; (5) the distal segment of the outer branch of the uropod is divided into a clear outer half and a dark inner half in *inornata*; in *perpensa* the inner half is suffused with dark pigment but there is no sharp line dividing inner and outer halves.

The synonymy given here is necessarily incomplete, for all of the many references to *S. oratoria* var. *inornata* and *S. oratoria* var. *perpensa* must be verified before an accurate synonymy can be compiled. All of the previous Australian records, which are summarized in the papers of Stephenson (1953, 1955, and 1962) and Stephenson and McNeill (1955), also must be verified.

There is a strong possibility that there are more than two species involved in this complex within the *Squilla oratoria* group that share an undivided dorsal ridge on the carpus of the raptorial claw. Kemp (1913) noted that there were some specimens examined by him in which the bifurcation of the median carina of the carapace was obsolete. The entire *S. oratoria* complex needs to be studied in detail.

Distribution.—This species is known with certainty from the south-western Pacific, from Singapore, Borneo, the Indo-Malayan area, and Queensland, Australia. Subtidal to moderate depths around 50 m.

Judging from the unpublished collections in the U.S. National Museum, *S. inornata* is one of the most common species of *Squilla* in the south-western Pacific.

Squilla interrupta Kemp, 1911

Fig. 4

Restricted synonymy:—

Squilla interrupta Kemp, 1911, p. 98; 1913, p. 72, pl. V, figs 60-62.—Holthuis, 1941, p. 253.—Stephenson, 1952, p. 7; 1953, p. 42.—Baig, 1954, p. 143 [listed].—Stephenson and McNeill, 1955, p. 244.—Stephenson, 1960, p. 61.

Squilla woodmasoni: Stephenson and McNeill, 1955, p. 243 [part][not *Squilla woodmasoni* Kemp, 1911].

Material.— 1 brk. ♀, CL 18.8; Queensland; C. E. Beddome, col.; MCZ 7887.—1 ♀, 90.4; Townsville, probably Cleveland Bay, Queensland; September 1952; G. Coates col.; exchange from Australian Museum; USNM 111356.—1 ♀, 105.5; Brisbane River (?), possibly obtained somewhere in Moreton Bay, Queensland; 9th June 1945; pres. J. S. Hynd; exchange from Australian Museum; USNM 111359.

Remarks.—All three specimens agree in all respects with published accounts. As noted by Holthius (1941), the spine formula for the abdominal carinae is as follows: submedian, 5-6; intermediate, 4-6; lateral, 3-6; marginal, 1-5.

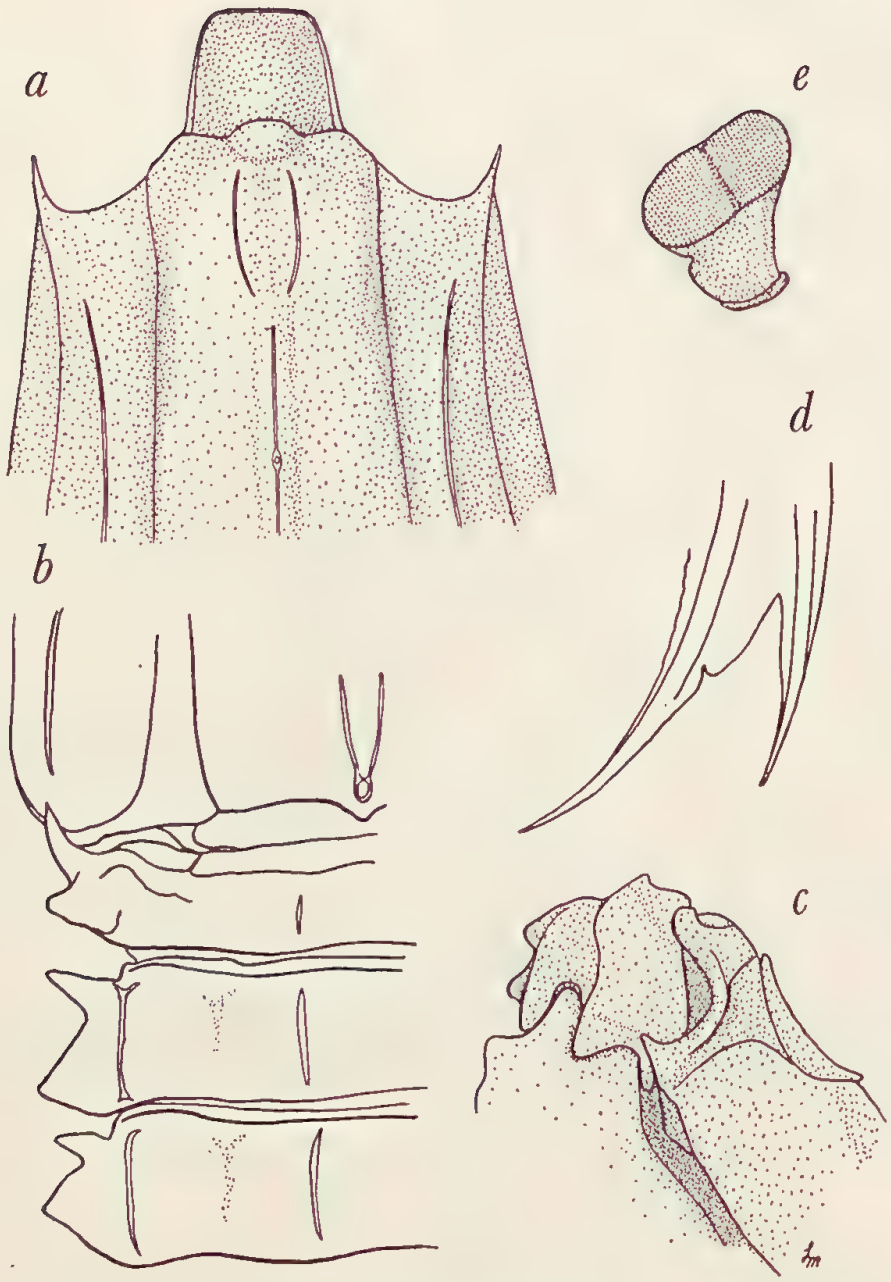

Fig. 4.—*Squilla interrupta* Kemp, female, TL 90.4 mm, Townsville. *a*, anterior portion of carapace and rostral plate; *b*, lateral processes of fifth, sixth, and seventh thoracic somites; *c*, carpus of raptorial claw; *d*, basal prolongation of uropod; *e*, eye.

The specimen from Cleveland Bay was reported by Stephenson and McNeill (1955) as *S. woodmasoni*.

Distribution.—Indian and western Pacific Oceans, from the Persian Gulf to Australia, Java, and Formosa. Shallow water, 20 m. or less. In Australia it has been recorded from Queensland and New South Wales (Stephenson and McNeill, 1955).

Squilla laevis Hess, 1865

Restricted synonymy:—

Squilla laevis Hess, 1865, p. 170, pl. vii, fig. 22.—Kemp, 1913, p. 49, pl. III, figs 35-37.—Stephenson, 1952, p. 6; 1953, p. 40.—Stephenson and McNeill, 1955, p. 242.—Stephenson, 1960, p. 61; 1962, p. 33.

Material.—1♂, 61.2; Parramatta River, Port Jackson, New South Wales; taken in prawn trawl; USNM 78429.—1♂, 78.2; Port Jackson, New South Wales; seined with haul of prawns; purchased; USNM 98875.

Colour.—(Not recorded previously.) Carinae and grooves of carapace dark; last three thoracic and all abdominal somites with posterior black line; lateral processes of sixth and seventh thoracic somites with dark spot; second and fifth abdominal somites with rectangular, black median patch, that on fifth almost divided into two submedian spots; carinae of marginal teeth and dorsal rows of pits on telson dark.

Remarks.—The rostral plate in these specimens is trapezoidal with the anterior margin transverse, not rounded as illustrated by Kemp (1913). Otherwise the specimens agree with Kemp's account in every respect.

Distribution.—Known only from Australia, from Queensland to Western Australia around the southern part of the continent. Shallow water, 10 m. or less.

Squilla mcneilli Stephenson, 1953

Squilla armata: Whitelegge, 1900, p. 199 [not *S. armata* H. Milne-Edwards, 1837].

Squilla mcneilli Stephenson, 1953a, p. 213, text-fig. 4.—Stephenson and McNeill, 1955, p. 242.—Stephenson, 1962, p. 34.

Material.—3♂, 54.3-66.5; 3♀, 64.0-67.4; N of Montague Island, New South Wales; 109 m; *Endeavour*; AM Reg. No. E. 6141.—1♂, 50.0; 3♀, 45.0-46.6; Great Australian Bight, S.W. of Eucla, Western Australia; Long. 126° E; 146 m; *Endeavour*; USNM 111376.—1♀, 88.2; (?) Norah Head S 40, W 15 miles; 82-106 m; *Endeavour*; AM Reg. No. E. 4505.

Remarks.—These specimens agree well with Stephenson's comprehensive original description. All specimens have four epipods. In two specimens, one raptorial claw is armed with six teeth; all of the others have five teeth on each claw. The number of denticles present on the telson is 11-16, 6-10, 1; Stephenson reported 14-17, 8-10, 1 in his original series. Three of the present specimens have posterior spines on the intermediate carinae of the first abdominal somite; usually this carina is unarmed. In the larger males the posterior margin of the telson is noticeably inflated, particularly at the bases of the marginal teeth.

Distribution.—Stephenson (1953a) recorded this species from numerous localities off New South Wales, at depths of 46-164 m, and more recently (1962) from Western Australia. All of the localities known are in Australian waters.

Squilla perpensa Kemp, 1911

Restricted synonymy:—

Squilla nepa: Miers, 1884, p. 298 [not *S. nepa* Latreille, 1825].

Squilla oratoria var. *perpensa* Kemp, 1911, p. 98; 1913, p. 70, pl. V, figs 57-59 [part].

Squilla anomala Tweedie, 1935, p. 45.—[?] Stephenson, 1952, p. 7; [?] 1953, p. 43.—[?] Stephenson and McNeill, 1955, p. 245.

Material.—2 damaged specimens; Hongkong; syntypes of *S. perpensa;* BM(NH) Reg. No. 1910.11.14.8-9.—1♂, 85.1; Siglap, Singapore; littoral; June 1934; M. W. F. Tweedie, col.; holotype of *S. anomala*; BM(NH) Reg. No. 1935.12.16.7.—1♂ 68.1; same; paratype of *S. anomala*; RNHL Reg. No. 397.—1,♀ 81.8; same;

paratype of *S. anomala*; RNHL Reg. No. 426.—1♂, 61.7; Port Darwin, N. Australia; 13-32 m; H.M.S. *Alert*; BM(NH) Reg. No. 82.7.

Remarks.—During a recent visit to the British Museum, syntypes of *S. perpensa* were compared with the holotype of *S. anomala*, and the latter was compared with a series of *S. perpensa* from various localities. No differences were found which could be used to separate *S. anomala* from *S. perpensa*, so it must be considered a synonym of the latter.

The types of both species each have a short, broad rostral plate, small eyes, and a slender anterior lobe on the lateral process of the sixth abdominal somite.

Tweedie (1935) clearly recognized that two distinct forms shared the undivided carpus on the raptorial claw, but concluded that *S. o. perpensa*, even though it had been illustrated as the species with a short rostral plate, was identical with *S. o. inornata*. The latter was characterized by Tweedie as a "variety" with a long rostral plate.

Since the material at the British Museum identified by Kemp contained both species (*perpensa* and *inornata*), it seems possible that both are represented in his type-series in the Indian Museum. If so, the selection of a lectotype will determine whether *S. perpensa* or *S. anomala* will be used for the species with the short rostral plate.

Differences between *S. inornata* and *S. perpensa* are summarized under the discussion of *S. inornata*.

Unfortunately, no specimens of *S. perpensa* are available at the time of this writing, so a diagnosis and illustrations cannot be provided here. Good illustrations, showing the main diagnostic features, have been provided by Kemp (1913, pl. V, figs 57-59).

As in *S. inornata*, all previous records of *S. perpensa* must be verified before an accurate synonymy can be given. The synonymy given here includes references to specimens seen by me, as well as Australian records which require verification. These latter are preceded by a question-mark.

Distribution.—Western Indo-Pacific, from Singapore and Australia to the Persian Gulf (Kemp, 1913). Moderate depths, 100 m or less.

Squilla woodmasoni Kemp, 1911

Fig. 5

Restricted synonymy:—

Squilla woodmasoni Kemp, 1911, p. 99; 1913, p. 74, pl. V, figs 63-65.—Holthuis, 1941, p. 255.—Gravely, 1941, pp. 73, 74.—Stephenson, 1952, p. 5 [part]; 1953, p. 42.—Kurian, 1954, p. 86.—Stephenson and McNeill, 1955, p. 243.—Chuang, 1961, p. 180, pl. 82.—Barnard, 1962, p. 244.

Material.—1 brk. ♂, ca. 155.0; 12 mi. NNE of Bowen, Queensland; 35-46 m; *Endeavour*; AM Reg. No. E. 3158.

Discussion.—This badly fragmented specimen differs from Kemp's account of this species in several important respects: (1) the anterior bifurcated portions of the median carina of the carapace are sharp and distinct; (2) the rostral plate, although short and truncate, is narrowed anteriorly; (3) the lobe on the outer margin of the inner spine of the basal prolongation of the uropod is well-defined; all of these differences are shown in fig. 5. Hansen (1926) and Holthuis (1941) reported specimens

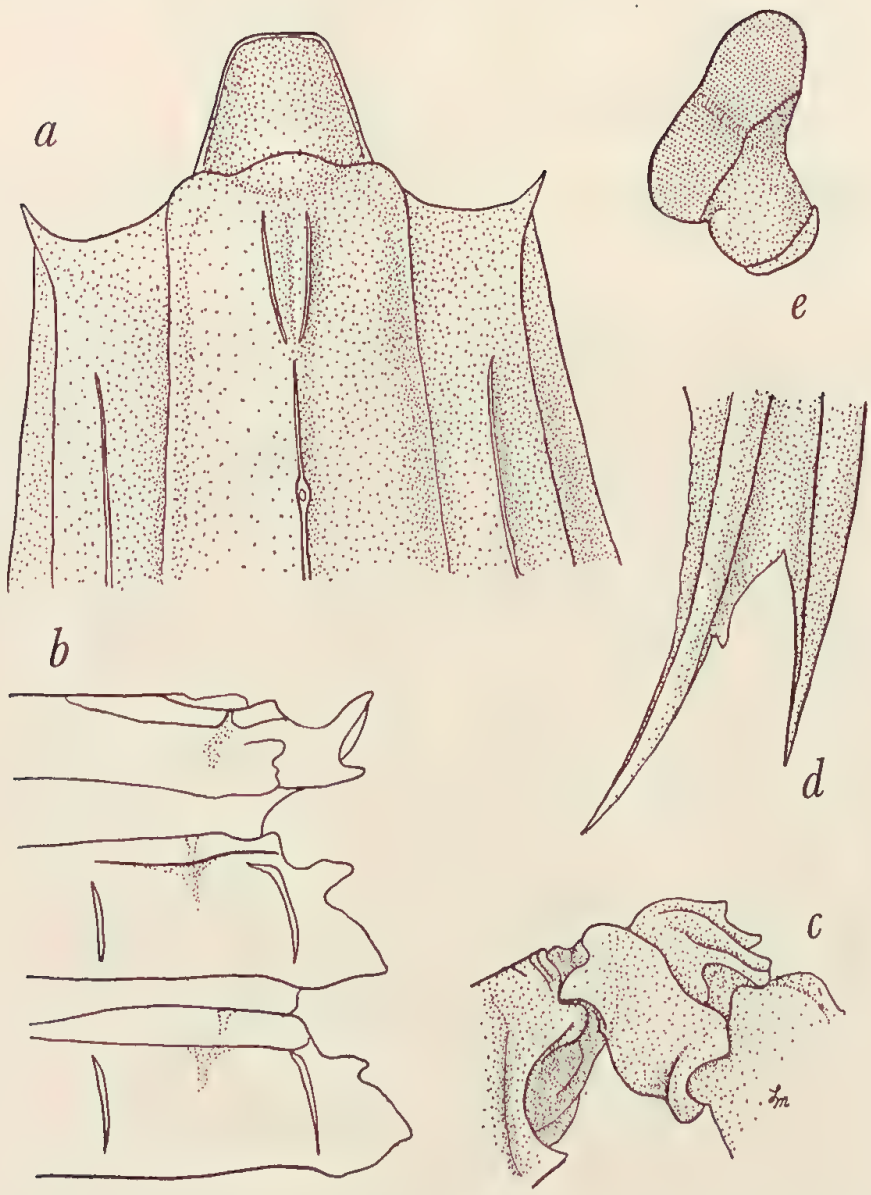

Fig. 5.—*Squilla woodmasoni* Kemp, male, TL ca. 155.0 mm, off Bowen. *a*, anterior portion of carapace and rostral plate; *b*, lateral processes of fifth, sixth, and seventh thoracic somites; *c*, carpus of raptorial claw; *d*, basal prolongation of uropod; *e*, eye.

with similar differences; Hansen's specimens also lacked the characteristic anterior spine on the ophthalmic somite. Since Kemp's material was mainly from the Indian Ocean, it seems possible that the Pacific specimens assigned to this species actually belong to a distinct species or subspecies. Kemp (1913) suggested that there might be a distinct subspecies in East Africa.

Distribution.—Western Indo-Pacific, from Japan and Australia through the Indian Ocean. In Australia it has been recorded from the Northern Territory, Queensland, New South Wales, and Western Australia (Stephenson and McNeill, 1955). Moderate depths, 50 m or less.

Hemisquilla Hansen, 1895

Hemisquilla ensigera (Owen, 1832)

Restricted synonymy:—

Gonodactylus ensiger Owen, 1832, p. 6.

Pseudosquilla stylifera: Whitelegge, 1900, p. 198.—Kemp, 1913, p. 106, pl. VII, figs 84-85, text.-fig. on p. 107.

Hemisquilla stylifera: Schmitt, 1940, p. 181 [discussion].—Stephenson, 1953, p. 43; 1955, p. 2.—Stephenson and McNeill, 1955, p. 253.

Hemisquilla ensigera: Manning, 1963b, p. 315.

Material.— 1, ♂ 138.0; near Tathra Head, near Moruya, New South Wales; 182-455 m; *Endeavour*; USNM 111374.— 1 ♀, 150.0; same; AM Reg. No. E. 4397.— 1 ♂, 155.0; Barren Island, New South Wales; 73 m; *Endeavour*; AM Reg. No. E. 4508.—1 damaged ♂, CL 27.0; 6 mi. SxE of Brush Island, New South Wales; 118 m; *Endeavour*; AM Reg. No. E. 2238.— 1 ♂, 157.0; eastern slopes, S of Gabo Is., Victoria; 200 m; *Endeavour*; AM Reg. No. E. 4794.— 1 ♂, 158.0; same; AM Reg. No. E. 4795.— 1 ♂, 158.0; same; AM Reg. No. E. 4796.—1 ♀, 156.0; S. of Mt Cann, Victoria; 109-146 m; *Endeavour*; USNM 111375.—1♂, 174.0; same; USNM 111371.—1 ♂, 135.0; same; 100-127 m; AM Reg. No. E. 6076.— 1 ♂, 142.0; S and SW of Mt Cann, Victoria; 127-182 m; *Endeavour*; USNM 111372.— 1 ♂, 169.0; same; AM Reg. No. E. 6100.—1 ♀, 153.0; S from Cape Everard, Victoria; 146-218 m; *Endeavour*; AM Reg. No. P. 3536.—1 ♂, 168.0; same; AM Reg. No. P. 3537.— 1 ♂, 174.0; SE of Cape Everard, Victoria; 127-146 m; *Endeavour*; AM Reg. No. E. 6098.—1 ♂, 137.0; off Cape Everard, Victoria; 109 m; *Endeavour*; AM Reg. No. E. 1317.—1 ♂, 145.0; same; 127 m; AM Reg. No. E. 2235.—1 ♂, 160.0; same; AM Reg. No. E. 2236.—1 ♀, 135.0; same; AM Reg. No. E. 2237.—1 ♀, ca. 140.0; same; 109 m; AM Reg. No. E. 1316.—1 ♂, 143.0; same; AM Reg. No. E. 1315.— 1♀, 143.0; same; USNM 111373.—1 ♂, 167.0; same; AM Reg. No. P. 2383.— 1♂, 146.0; Bass Strait, Victoria; *Endeavour*; AM Reg. No. E. 441.—1 ♂, 164.0; same; AM Reg. No. E. 442.—1 ♀, 127.0; eastern edge Bass Strait, Gabo to Gable Is., Victoria; 109-182 m; *Endeavour*; AM Reg. No. P. 3541.—1 ♂, 145.0; Disaster Bay, Tasmania; *Endeavour*; AM Reg. No. E. 4503.

Remarks.—The status of the Australian specimens of this species and their relation to the western American populations are currently being investigated by W. Stephenson.

Distribution.—Discontinuously distributed in the Pacific, with populations along the west coast of America and off Australia and Tasmania. In Australia it has been reported from New South Wales, Victoria and Tasmania in depths to 455 m (Stephenson and McNeill, 1955).

Manningia Serène, 1962

Manningia Serène, 1962, p. 20.

Remarks.—This genus was erected by Serène for *Pseudosquilla pilaensis* de Man 1888, which is rather rare and has been recorded only a few times since its original description. A survey of the few published illustrations of *M. pilaensis* has revealed a number of inconsistencies which seem to indicate that all of the known specimens should be re-examined to determine whether more than one species may be involved. The Australian record for *M. pilaensis* is based on the new species described below. It is hoped that a redescription of *M. pilaensis* accompanied by adequate illustrations can be completed at an early date.

The holotype of the new species described below was found among the small collection of stomatopods obtained by the Arnhem Land Expedition; one of the paratypes had been reported by Stephenson (1953) as *M. pilaensis*.

Manningia notialis, new species

Fig. 6

Pseudosquilla pilaensis: Stephenson, 1953, p. 44.—Stephenson and McNeill, 1955, p. 245 [not *M. pilaensis* (de Man, 1888)].

Holotype.—1♀, 63.0; ironstone reef (not coral) at Yirrkala, NW of Cape Arnhem, Northern Territory; Arnhem Land Exped. Sta. M48-21; emulsifiable rotenone; 6th August 1948; R. R. Miller and natives, col.; AM. Reg. No. P. 14788.

Paratype.—1 damaged ♂, ca. 50.0; Bowen, Queensland; ?.2.1934; J. MacGregor, don.; Queensland Museum Reg. No. W. 1782.—1♂, 52.9; Weipa, Gulf of Carpentaria, Queensland; dredged, 9 m, in silt; 9th July 1961; G. Webster, col.; exchange from Australian Museum; USNM 112436.

Description.—Cornea strongly bilobed, set very obliquely on stalk, outer margin of eye longer than inner; eyes not extending to end of first segment of antennular peduncle; ophthalmic somite and base of eyes completely covered by rostral plate; eye-scales truncate, separate.

Antennular peduncle two-thirds or more as long as carapace.

Antennal scale slender, elongate, curved, margins completely setose; antennal protopod with 1 ventral papilla.

Rostral plate pentagonal, without apical spine; apex sharp but obtuse; length of plate about two-thirds greatest width.

Carapace smooth, narrowed anteriorly, without spines or carinae except for short marginal carinae present on posterior margin of each lateral plate.

Raptorial claw stout; dactylus armed with 4 teeth, outer margin with strong basal notch; propodus broad, superior margin fully pectinate; carpus with 2 teeth on upper margin; merus lacking inferodistal spine.

Propodus of each of last 2 maxillipeds about as long as broad, that of fifth maxilliped longer than broad, with prominent distal brush of setae, more pronounced than on either of 2 preceding maxillipeds.

Mandibular palp and 5 epipods present.

Fifth thoracic somite with blunt, inconspicuous lateral process; lateral processes of next 2 somites rounded, that of seventh somite flattened laterally; last 3 thoracic somites each with 1 pair of dorsal carinae; inner branches of walking legs very slender, two-segmented; eighth thoracic somite with low, blunt median keel.

Abdomen smooth, flattened, distinct carinae present on last 2 somites only; second to fifth somites with lateral, longitudinal grooves, not flanked with sharp carinae; fifth somite with 3 pairs of lateral carinae, upper at level of lateral carina of last somite; other carinae, on each side, between upper carina and ventral margin, lower not on margin; middle carina short, oblique, not extending to posterior margin; fourth and fifth somites with posterolateral spines; sixth somite with 3 pairs of carinae, all armed posteriorly, submedians and intermediates broad, laterals terminating at base of lateral spine; sixth somite with inconspicuous ventral spine in front of articulation of uropod.

Telson much broader than long, with 3 pairs of marginal teeth, submedians with appressed bases and movable apices; submedian denticles absent; 2 broad intermediate denticles, outer with ventral spine, and 1 broad lateral denticle, with

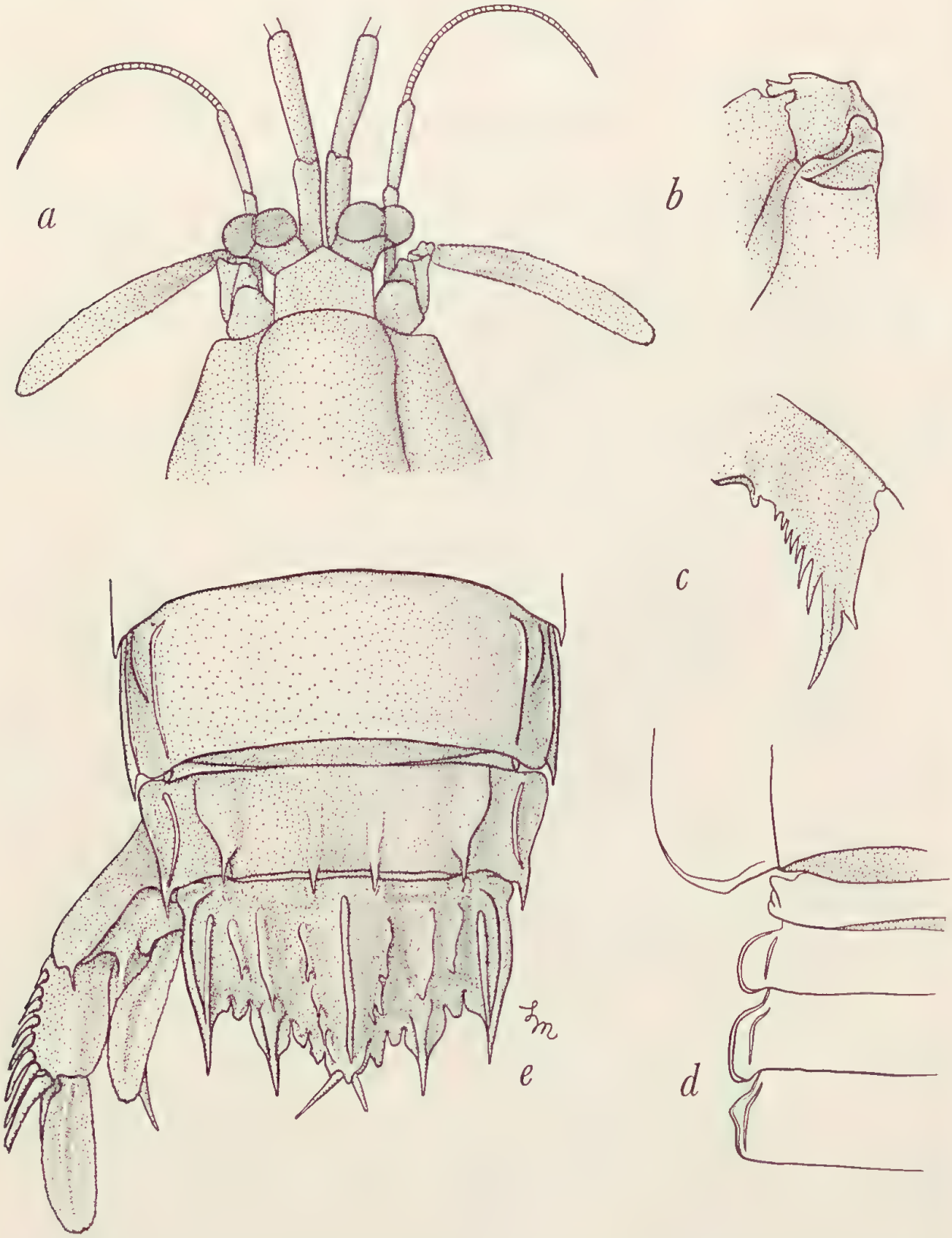

Fig. 6.—*Manningia notialis*, new species, female holotype, TL 63.0 mm, Yirrkala. *a*, anterior portion of body; *b*, carpus of raptorial claw; *c*, basal prolongation of left uropod, ventral view; *d*, lateral processes of exposed thoracic somites; *e*, last two abdominal somites, telson, and left uropod.

ventral spine; dorsal surface with median and 5 pairs of lateral carinae; inner pair of carinae interrupted, divided into 3 portions, each spined; next 2 carinae uninterrupted, terminating in blunt teeth; outer 2 carinae converging on lateral tooth; submedian teeth each with short, irregular, dorsal carina; postanal keel absent.

Uropod with 8-9 movable spines on outer margin of penultimate segment of outer branch, last extending well past midpoint of distal segment; inner branch broad, curved, outer margin convex; inner spine of basal prolongation longer than outer, armed with 7-8 fixed, graded spines on inner margin, distal the largest; no broadly-rounded lobe present between spines of basal prolongation.

Colour.—Largely faded in the present material. The holotype has inconspicuous dark chromatophores scattered over the body in no fixed pattern.

Measurements.—Female holotype, TL 63.0 mm; other measurements, in mm: carapace length, 13.7; cornea width, 3.2; rostral plate length, width, 2.2, 3.4; telson length, width, 7.6, 11.1.

Discussion.—*M. notialis* is very similar to *M. pilaensis* but can be distinguished from that species by the following features: (1) the rostral plate is unarmed anteriorly; (2) the inferodistal angle of the merus of the raptorial claw is unarmed; (3) the third lateral carinae of the telson are not interrupted; (4) there is no swollen area between the submedian and intermediate carinae of the sixth abdominal somite; and (5) the inner branches of the walking legs are slender on all the legs, whereas in *M. pilaensis* they are broad on the sixth legs, slenderer on the seventh and eighth. The single specimen of *M. pilaensis* available for comparison has two papillae present on the antennal protopod, one ventral and one mesial. The types of *M. notialis* each have but one ventral papilla. The absence of the rostral spine and that on the merus of the claw will immediately distinguish this species from *M. pilaensis*.

Name.—The specific name is from the Latin, *notialis*, southern, referring to the distribution of the species.

Distribution.—Yirrkala, Arnhem Land, and Bowen and Gulf of Carpentaria, Queensland.

Odontodactylus Bigelow, 1893

Odontodactylus cultrifer (White, 1850)

Restricted synonymy:—

Gonodactylus cultrifer White, 1850, p. 96, pl. 16, figs 1-2.

Gonodactylus carinifer Pocock, 1893, p. 478, pl. 25, figs 4-4b.

Odontodactylus cultrifer: Kemp, 1913, p. 137.—Stephenson, 1952, p. 10; 1953, p. 46.—Serène, 1954, pp. 6, 8, 11, 13, 17, 72, pl. 6, figs 5-6.—Stephenson and McNeill, 1955, p. 248.—Stephenson, 1962, p. 35.

Odontodactylus mindanaoensis Roxas and Estampador, 1930, p. 115, pl. IV.

Odontodactylus cultrifer var. *tridentata* Serène, 1954, pp. 6, 7, 8, 72, pl. 6, figs 7-8.

Material.—1 brk. ♂, 125.4; 10 mi. NW of Bustard Head, off Port Curtis Queensland; 29 m; *Endeavour*; AM Reg. No. E. 3154.—1 brk. ♀, 106.5; Platypus Bay, Queensland; 13-16 m; *Endeavour*; USNM 111380.—1♀, 118.2; same; *Endeavour*, No. 1, haul 2; 28th July 1910; AM Reg. No. P. 3549.

Discussion.—I follow Hansen (1926) in synonymizing *O. carinifer* (Pocock), which is based upon a juvenile specimen, with *O. cultrifer*. There is also little reason to recognize *O. mindanaoensis* Roxas and Estampador from the Philippines, for the description of that species agrees in all respects with previous accounts of *O. cultrifer* as well as with the present material. *O. cultrifer* var. *tridentata* Serène is also synonymized here with *O. cultrifer*. The main distinguishing feature of *tridentata* appears to be the presence of three teeth on the dactylus of the raptorial claw. As noted below, specimens of this species may have two, three or four teeth on the claw.

The rostral plate of this species is trapezoidal, with the anterior margin strongly deflexed. The number of teeth on the dactylus of the raptorial claw is variable, from two on the right and three on the left, three right and left, to three right, four left. On the ischium of the claw there is a high ventral crest armed with an anterior tubercle. The outer margin of the proximal segment of the uropodal outer branch may be armed with eight to 10 teeth. The characteristic high crest of the telson is noticeably higher in males than females; the telson width/crest height ratio is 2.35 in the male, 3.81-4.04 in the two females. In both females the dorsal submedian carinae of the telson merge with the carinae of the submedian marginal teeth; in the male the carinae are interrupted.

The trapezoidal rostral plate, the small number of teeth on the claw, the absence of the posteriorly-reflected portions of the submedian carinae of the sixth abdominal somite, and the high crest of the telson will serve to distinguish this species from all others in the genus. The only other species of the genus reported from Australian waters, *O. scyllarus* (Linnaeus) and *O. japonicus* (de Haan), both have two convergent carinae on either side of the median crest of the telson; only one carina on each side is found in *O. cultrifer*.

Remarks.—A complete redescription of this species and a review of the genus are in preparation. A study of the specimens reported herein as well as material from numerous other sources indicates that several of the currently-recognized species are juveniles of other, established species.

Distribution.—Indo-Pacific, from China, Viet Nam, Australia, and the Gulf of Siam. In Australia it has been recorded from Queensland and Western Australia (Stephenson and McNeill, 1955; Stephenson, 1962), in moderate depths, 36 m or less.

Protosquilla Brooks, 1886

Protosquilla Brooks, 1886a, p. 84.

Gonodactylus "Group III" Kemp, 1913, p. 146.

Remarks.—Five species of *Protosquilla* are now known to occur in Australian waters, *P. trispinosa* (Dana, 1852), *P. glyptocerca* (Wood Mason, 1875), *P. pulchella* (Miers, 1880), *P. stoliura* (Muller, 1886), and *P. tweediei* (Serène, 1952). Australian records for these species have been summarized by Stephenson and McNeill (1955) and Stephenson (1962).

While visiting the British Museum in June, 1964, I was able to examine the specimens from Shark's Bay, Western Australia, reported by Miers (1880, 1880a) as *Gonodactylus trispinosus*. Both are males (TL 37.8-45.0; BM(NH) Reg. No. 58.172) and, as suggested by Pocock (1893) who quoted Hansen's re-identification, both are *P. stoliura* (Muller). Stephenson and McNeill (1955, p. 476) noted that this species had "not previously been recorded with certainty from Australian waters". Those authors also had one specimen from Western Australia, and other specimens from the same area are mentioned by Stephenson (1962).

Gonodactylus Berthold, 1827

Remarks.—The Indo-Pacific species of this genus, which probably provides the greatest number of difficult problems for the systematist, have been the subject of several detailed studies, the results of which have been most ably summarized by Kemp (1913). Since the publication of that paper the nomenclature of the species and "varieties" recognized by him has remained relatively stable. To some extent this has been due to a general "lumping" of morphologically different forms into species which Kemp treated. Hansen (1926), for example, regarded several of the then recognized species as variants of the most common species, *G. chiragra* (Fabricius). Few taxonomists have gone as far as Hansen or the other extreme, which was advocated by Lanchester (1903), recognition of many named or lettered varieties.

The species in *Gonodactylus* are difficult to work with because they all superficially resemble each other; many of the characters that have been shown to be reliable in other genera, such as the armature of the raptorial claw, carination of the carapace, shape of the lateral processes of exposed thoracic somites, carination and spination of the abdomen, and marginal armature of the telson, among others, are either totally lacking in *Gonodactylus* or are essentially identical in all of the species. In the past, specific differences have been based largely on subjective evaluations of the few varying features that are available. Thus in one species anterolateral angles on the rostral plate are rounded, in another they are acute, and in a third they are spiniform; these are reliable characters, but they are difficult to assess without comparative material. However, there are other characters that are more useful, some of which have not been applied to *G. chiragra* and its close relatives in the Indo-Pacific. Among the features that can be used to separate these species are the colour pattern, the shape and size of the eye-scales, the shape of the rostral plate, the relative width of the abdomen, the shape and carination of the telson, and the shape of the uropodal inner branch. Perhaps the most important of these is colour, which is diagnostic for *G. platysoma* and *G. smithii*. Another feature which may be of importance is habitat. Some of these characters may be sexually dimorphic, including overall colour and colour pattern as well as telson and rostral plate form. Serène (1954) has recently provided some interesting observations on sexual dimorphism in this and several other species of stomatopods.

In his discussion of variation in *G. chiragra*, Kemp (1913) pointed out that small specimens exhibited more variation than larger ones. Among the possible explanations suggested by Kemp were (1) the existence of dwarf races, (2) loss of variation through growth, and (3) greater mortality rate for variable forms. Kemp apparently believed that the first and third explanations were improbable and was inclined toward the explanation of loss of variation through growth. Bigelow (1931) suggested that there were good reasons for investigating the existence of dwarf races, and more recently Serène (1954) named a dwarf race ("race naine"), *G. chiragra* var. *viridis*, from Viet Nam. Serène's variety is mature at 30 mm and ovigerous at 35 mm; further, it differs in colour and morphology from specimens of *G. chiragra* from the same area. In view of the other evidence given by Serène, I can see no reason for not recognizing his "race naine" as a distinct species.

In view of the limited amount of material available for this study, it is not possible to undertake any extensive revision of Indo-Pacific *Gonodactylus* here; such a revision is badly needed. *G. platysoma* Wood-Mason and *G. smithii* Pocock are recognized and briefly characterized. The former, which is usually regarded as a variety of *G. chiragra*, has a similar geographic range to that species and is distinct throughout its range; it must be treated as a distinct species. *G. smithii* is also a distinct species, and is probably not conspecific with *G. acutirostris* de Man, as suggested

by Serène (1954). *G. chiragra* is only treated briefly below, and notes on *G. falcatus* (Forskål) and *G. graphurus* Miers are included.

The genus *Gonodactylus* as used here is restricted to *Gonodactylus* Group I of Kemp (1913). Kemp's Group II is *Mesacturus* Miers, Group III is *Protosquilla* Brooks, and Group IV is *Hoplosquilla* Holthuis. Holthuis (1964) has commented briefly on these genera, and a more extensive treatment is in press (Holthuis and Manning).

KEY TO AUSTRALIAN SPECIES OF GONODACTYLUS

1. Central area of telson with 5 longitudinal carinae..... 2
   Central area of telson with 3 longitudinal carinae..... 3
2. First 5 abdominal somites each with a fine transverse groove.... *graphurus*, p. 108
   Abdominal somites not grooved ..... *falcatus*, p. 109
3. Eye-scales, broad, extending laterally to anterolateral angles of rostral plate; lateral teeth of telson suppressed ..... *platysoma*, p. 110
   Eye-scales narrow; lateral teeth of telson distinct..... 4
4. Anterolateral angles of rostral plate sharp; uropodal inner branch convex on inner margin ..... *smithii*, p. 112
   Anterolateral angles of rostral plate rounded; uropodal inner branch sinuous on inner margin ..... *chiragra*, p. 113

Gonodactylus graphurus Miers, 1875 (*sensu* Brooks, 1886)

Restricted synonymy:—

Gonodactylus graphurus: White, 1847, p. 85 [part; *nomen nudum*].

Gonodactylus graphurus: Miers, 1875, p. 344 [part; reference to part of White's material only].—Brooks, 1886, p. 58, pl. XIV, figs 1, 4, 6, pl. XV, figs 3, 8.—Kemp, 1913, p. 169, text-fig. 1 on p. 170.—Stephenson, 1952, p. 12; 1953, p. 47.—Stephenson and McNeill, 1955, p. 250.—Stephenson, 1962, p. 35.—Ingle, 1963, p. 29 [discussion].

Material.—1♂, 42.7; Prince of Wales Island, Queensland; 13th September, 1913; H. L. Clark, col.; MCZ.—1♂, 72.3; 18 mi. SW x S of Lady Elliott Island, off Queensland; 46-47 m; *Endeavour;* USNM 111378.—1♀, 38.2; same; in sponge; 33 m; *Endeavour;* USNM 111377.—4 spec., fragmented; Pine Peak, Queensland, S 29E; *Endeavour*; AM Reg. No. P. 3571.—1♂, 22.0; 4♀, 27.2-52.8; 11-14 mi. NW of Pine Peak, Queensland; 44-47 m; *Endeavour*; AM Reg. No. E. 3187.

Diagnosis.—Rostral plate with acute anterolateral angles; eye-scales small, erect; first to fifth abdominal somites each with fine transverse groove, interrupted along midline on posterior somites, situated just behind midpoint on each somite; on lateral portions of abdomen, grooves turn anteriorly, terminating in prominent, anterior pit; second, third and fourth somites each with oblique, ventrally-directed groove extending for short distance from pit; first somite lacking this groove; fifth somite with groove directed posteriorly, not ventrally; first five somites also with third oblique, longitudinal groove on pleura, not connected to ventrally-directed groove; sixth abdominal somite, telson, and uropod as in *G. falcatus*.

Colour.—Completely faded in these specimens.

Size.—Males, TL 22.0-72.3 mm; females, TL 27.2-52.8 mm.

Discussion.—The presence of the fine grooves across the abdominal somites immediately distinguishes this species from *G. falcatus*, which it otherwise resembles rather closely. The grooves are visible although incomplete in the smallest specimen examined, a male, TL 22.0 mm. A good illustration of the pattern of grooves on the abdomen has been given by both Brooks (1886) and Kemp (1913).

In his discussion of the past confusion between this species and *G. falcatus*, Ingle (1963) pointed out that the Samoan specimens recorded by Miers (1875) as *G. graphurus* were actually *G. falcatus*, and, further, that part of White's (1847) original series was also *falcatus*. L. B. Holthuis brought up in a discussion (in *litt.*) of this problem that since Miers referred to White, White's material must be considered part of the type-series; thus selection of a lectotype from White's specimens will determine whether or not the name *graphurus* can be retained for the species. R. W. Ingle of the British Museum (Natural History) is preparing a redescription of the species and will settle the problem in that paper.

Distribution.—Although there are numerous references to *G. graphurus* in the literature, there are no documented records of its occurrence west of the Indo-Malayan area. Pocock (1893) recorded specimens from the Arafura Sea and several Australian localities. Both Brooks (1886) and Kemp (1913) had material from Australia; recent records from that area have been summarized by Stephenson and McNeill (1955). All records in the literature, including those from Australia, need to be verified.

Gonodactylus falcatus (Forskål, 1775)

Restricted synonymy:—

Cancer falcatus : Forskål, 1775, p. 96.

Gonodactylus graphurus Miers, 1875, p. 344; 1880, p. 120, pl. III, fig. 9 [not *G. graphurus* White, 1847 (*nomen nudum*)].

Gonodactylus glabrous : Brooks, 1886, p. 62, pl. XIV, fig. 5, pl. XV, figs 7, 9.—Kemp, 1913, p. 167, pl. IX, fig. 113, text-fig. 2 on p. 170.—Bigelow, 1931, p. 127, text-fig. 1.—Armstrong, 1941, p. 14.—Barnard, 1950, p. 863, text-fig. 3f.—Dawydoff, 1952, p. 145.—Taramelli, 1955, p. 45.

(?) *Gonodactylus glabrous* var. *ternatensis* : de Man, 1902, p. 914, pl. XXVII, fig. 67.

Gonodactylus falcatus: Holthuis, 1941, p. 284, text-fig. 9a.—Tweedie, 1949, p. 40; 1950, p. 140.—Stephenson, 1952, p. 11; 1953, p. 47.—Holthuis, 1953, p. 61.—Serène, 1954, p. 79, pl. IX, text-fig. 13-6.—Stephenson and McNeill, 1955, p. 249.—Stephenson, 1962, p. 34.—Manning, 1962, p. 4.—Ingle, 1963, p. 29, figs 28, 57.

not *Gonodactylus glabrous:* Tokioka, 1953a, p. 143, text-fig. 1B [?=*Mesacturus spinosocarinatus* (Fukuda)].

(?) *Gonodactylus falcatus* var. *ternatensis:* Serène, 1954, p. 80, pl. 4, figs 7-12, pl. 10, text-fig. 13-7, 8.

Material.—1♂, 41.4; Green Island, near Cairns, Queensland; coral reef flat; USNM 107786.—1♂, 41.2; Bait Reef, E of Hayman Island, Cumberland Group, Queensland; USNM 107787.—1♀, 52.9; North West Island, Capricorn Group, Queensland; 1953; J. K. Howard, col.; USNM 96973.—5♂, 23.5-52.0; 4♀, 37.7-51.4; same; reef; December, 1925; USNM 64659.

Diagnosis.—Rostral plate with rounded anterolateral angles; eye-scales small, erect; abdomen without trace of transverse grooves, each somite with conspicuous lateral pit on each side; sixth abdominal somite with 6 carinae, usually spined, submedians and intermediates elevated, sharp laterally, tapering posteriorly, usually

excavate under marginal spines; lateral carinae of sixth somite narrower, interrupted anteriorly; short median carina usually present on sixth somite; telson with central group of 5 carinae, median and accessory medians usually spined and excavate posteriorly, anterior submedians usually unarmed and not excavate; 1 pair of short, oblique ridges converge but do not meet posterior to cluster of median carinae; anterior margin of telson with sharp tubercle on either side at level of intermediate spine of sixth somite; submedian and intermediate teeth of telson with long dorsal carinae, submedians each with ventral carina also; lateral tooth distinct, carinate laterally; postanal median carina present on ventral surface; inner branch of uropod slender, tapering distally, inner margin convex proximally, concave distally, setae of outer margin erect; outer spine of basal prolongation of uropod with prominent, acute lobe at base of inner margin.

Colour.—Two recently collected males (USNM 107786-7) mottled green, with dark, irregular bars across carapace and body somites; merus of claw with 3-4 dark bars; sixth abdominal somite with anterior pair of dark spots, one between each submedian and intermediate carina; telson with anterior pair of dark spots, one on each side at level of intermediate tooth of sixth abdominal somite.

Size.—Males, TL 23.5-52.0 mm; females, TL 37.7-52.9 mm.

Discussion.—A diagnosis of this well-known and very common species may seem superfluous, but in view of the obvious confusion in the past between this species and the closely related *G. graphurus* Miers, and in view of the distinct possibility that *G. falcatus* is made up of two or more species, it seems worthwhile to note the major features of these Australian specimens. All correspond with *G. falcatus ternatensis* (de Man), as defined by Serène (1954), but until more is known about geographic, morphological, and sexual variation it seems best to simply record these specimens as *G. falcatus*. Kemp (1913) and Bigelow (1931) both commented upon the variation in their specimens and neither recognized subgroups within the species. Serène (1954) has reported two morphologically distinct forms from Viet Nam, one of which he recognized as *G. falcatus ternatensis*, a "dwarf race". The possibility that more than one species is involved cannot be overlooked.

Both Brooks (1886) and Kemp (1913) have illustrated the differences between *G. falcatus* (as *G. glabrous*) and *G. graphurus* (Miers, sensu Brooks, 1886). None of the present specimens show any trace of the transverse grooves on the first five abdominal somites which are characteristic for *G. graphurus*.

Distribution.—Widely distributed in shallow water through the Indo-Pacific from Japan through Oceania and the Indian Ocean into the Red Sea; it has also been recorded from the Mediterranean (Holthuis, 1941).

Gonodactylus platysoma Wood-Mason, 1895

Restricted synonymy:—

Gonodactylus platysoma Wood-Mason, 1895, p. 11, pl. III, figs 3-9.—Manning, 1962, p. 3.

Gonodactylus chiragra var. *platysoma:* Kemp, 1913, p. 162, text-fig. 1 on p. 161; 1915, p. 180.—Bigelow, 1931, p. 117, pl. 1, fig. 2, pl. 2, fig. 2 [and synonymy].—Holthuis, 1941, p. 28 [and synonymy].—Tweedie, 1950, p. 140.

Gonodactylus chiragra: Stephenson and McNeill, 1955, p. 250 [part].—Gillett and McNeill, 1963, pl. 105 on p. 108 [colour plate].

Gonodactylus chiragra platysoma: Ward, 1942, p. 57.—Holthuis, 1953, p. 62.

Material.—1 brk. ♀, CL 15.5; North Australia; December, 1908; AM Reg No. P. 1761.—1 ♀, 78.8; same AM Reg. No. P. 1762.—1 ♂, 82.9; Murray Is., Torres Straits; 30th August-3rd October, 1907; Hedley and McCulloch, col.; AM Reg. No. P. 3131.—1 ♂, 88.2; same; AM Reg. No. P. 3132.—1 ♀, 68.7; same;

AM Reg. No. P. 3135.—2 ♂, 48.0-61.4; outer edge, St Crispin Reef, off Point Douglas, Queensland; September 1918; A. R. McCulloch, col.; AM Reg. No. P. 4297.—1 brk. ♀, 84.2; Green Is., near Cairns, Queensland; August, 1913; A. R. McCulloch, col.; AM Reg. No. P. 3846.—1 ♀, 84.0; Coates Reef, Queensland; April, 1925; Dr W. E. J. Paradice, pres.; AM Reg. No. P. 8032.—1 ♂, 88.3; reef, North West Is., Capricorn Group, Queensland; April, 1926; G. P. Whitley, pres.; AM Reg. No. P. 8581.—1 ♂, 53.6; Great Barrier Reef; British Great Barrier Reef Expedition 1928-1929; BM(NH) Reg. No. 1937.9.21.424.

Diagnosis.—Anterolateral angles of rostral plate rounded; eye-scales broad, extending to or beyond anterolateral angles of rostral plate, projecting laterally, dorsal margin irregular; abdomen broad, AWCLI 844-1038, usually over 910, mean 953 [n=7]; carinae of sixth abdominal somite slender or slightly swollen, usually armed posteriorly; median carina of telson broad, not sharp, rarely inflated or armed posteriorly; anchor absent; telson with 2 pairs of broad marginal teeth, laterals absent; inner branch of uropods elongate, tapering, inner margin sinuous.

Colour.—Body mottled green; in preservative, sixth thoracic and first abdominal somites with median black patch, lateral dark patches usually present on eighth thoracic somite and always on fifth abdominal somite.

An accurate coloured illustration of *G. platysoma* was published by Gillett and McNeill (1963).

Size.—Males, TL 48.0-88.3 mm; females, 68.7-84.2 mm. Kemp (1915) has recorded a male of 110 mm and a female of 99 mm.

Discussion.—With the exception of the specimen from the Great Barrier Reef Expedition which was in the collection of the British Museum, all of the above material is from the Australian Museum and was treated as *G. chiragra* by Stephenson and McNeill (1955). They noted that these specimens approached *platysoma* as defined by Kemp (1913) but that there was some variation in the breadth/length ratios of the body. For this and other reasons they concluded that the separation of *platysoma* as a varietal form could not be justified. Body breadth/length ratios were calculated from the abdominal width and the total length, as did Kemp in 1913.

Later, Kemp (1915) pointed out that the use of total length for this ratio could lead to inaccuracies because total length is variable, dependent upon the contraction or expansion of the body at the time of preservation. He again calculated length/breadth ratios, but this time used carapace length. Again, he could show complete separation on the basis of this character alone.

I have examined specimens of *G. platysoma* from many localities in the Indo-Pacific and I have seen no evidence of intergradation, in colour pattern or morphological features, between it and *G. chiragra*. *G. platysoma* can be distinguished from *G. chiragra* by the following features: (1) the eye-scales are much broader, extending to or beyond the anterolateral angles of the rostral plate; (2) the body is broader, the AWCLI varying between 844-1038, usually over 910; (3) there is no anchor on the posterior end of the median carina of the telson; (4) the median carina is never armed posteriorly; and (5) the lateral teeth of the telson are entirely suppressed. In view of these differences and the almost identical geographic ranges of *platysoma* and *chiragra*, I can see no reason for not recognizing *platysoma* as a distinct species.

Remarks.—The second largest specimen of *platysoma* examined, a male (TL 88.2 mm), was the slenderest, with an AWCLI of 844. This falls just below the upper limit (855) found for *G. chiragra*; specimens of *G. chiragra* of similar size (male, TL 80.2; female, TL 87.8) have an AWCLI of 781 and 756, respectively. Although there is overlap between these two species in the relative width of the body when all sizes are considered, when specimens of similar size are compared *G. platysoma* is always found to be broader.

Distribution.—*G. platysoma* has been recorded in the Indo-Pacific at localities ranging from Japan and Australia and the western Indian Ocean. It has not been recorded from the Hawaiian Islands or the Red Sea. Shallow water, on coral reefs.

Gonodactylus smithii Pocock, 1893

Restricted synonymy:—

Gonodactylus smithii Pocock, 1893, p. 475, pl. XXB, fig. 1.—Serène, 1954, pp. 6-7, 76, pl. VIII.

Material.—1 ♂, 27.1; 1 ♀, 19.1; Arafura Sea; H.M.S. *Penguin;* P. W. Bassett-Smith, col.; syntypes; BM(NH) Reg. No. 1892.4.18.231-232; 1 ♀, 74.0; Australia; BM(NH) Reg. No. 51.24.—1 ♂, 59.2; Murray Island, Torres Strait; 30th August-3rd October, 1907; Hedley and McCulloch, col; AM (in with *G. platysoma*, Reg. No. P. 3135).—2 ♂, 27.7-60.2; ironstone reef (not coral) at Yirrkala, NW of Cape Arnhem, Northern Territory; Arnhem Land Exped. Sta. M48-21; emulsifiable rotenone; 6th August, 1948; R. R. Miller and natives, col.; AM.—1 ♂, 52.6; same; USNM 111370.—1 ♂, 64.6; coral reef, Yirrkala, Arnhem Land, Northern Territory; Arnhem Land Exped. Sta. M48-21 (?); 12th August, 1948; USNM 111368.—1 brk. ♂, CL 18.8; 3 ♀, 59.6-71.8 (in 2 lots); Great Barrier Reef, Queensland; British Great Barrier Reef Expedition, 1928-1929; in with *G. chiragra*, BM(NH) Reg. No. 1937.9.21.414-423.—1 ♀, 57.0; Green Island, near Cairns, Queensland; coral reef flat; 1953; J. K. Howard; USNM 111381.—1 ♂, 73.5; 3 ♀, 63.2-67.8; Hook Reef, E of Hayman Island, Cumberland Group, Queensland; 1953; J. K. Howard; USNM 96972.—1 ♀, 69.2; Bass Strait (?), Victoria; *Endeavour;* AM Reg. No. E. 3140.

Diagnosis.—Rostral plate with anterolateral angles acute, sharp, but not spinous; eye-scales of moderate size, broader than high but not expanded laterally; body slender, AWCLI 750-806, mean 769 [n=7]; carinae of sixth abdominal somite sharp, apices usually spined; telson usually longer than broad, width occasionally subequal to length; median carina of telson usually sharp, apex spined, accessory median carinae sharp distally, converging under apex of median carina to form anchor; anterior submedian carinae sharp, apex acute but not always spinous; anterior surface of telson with noticeable tubercle under intermediate spine of sixth abdominal somite; submedian and intermediate marginal teeth of telson sharp, slender, with sharp dorsal carinae; lateral teeth of telson small but distinct; inner margin of inner branch of uropod evenly convex.

Colour.—In preservative, mottled green, with body segments outlined posteriorly and carinae of sixth abdominal somite and telson outlined with dark green; dactylus of claw bright pink, propodus with deep blue distal spot, merus with reddish distal dorsal pit, proximal edge of pit with black spot.

Size.—Males, TL 27.1-73.5 mm; females, TL 10.1-74.0 mm.

Discussion.—This species has long been synonymized with *G. chiragra* (Fabricius), which it closely resembles. However, specimens of *G. smithii* can be separated from *chiragra* by the following features: (1) the anterolateral angles of the rostral plate are acute, not rounded; (2) the carinae of the telson are sharp, with the median carina usually terminating in a slender spine; (3) the inner branch of the uropod is short and broad, with the inner margin evenly convex; (4) the dactylus of the claw is red or pink, the distal portion of the propodus is deep blue, and there is a bright red subdistal spot on the inner, dorsal margin of the merus.

The specimens of *G. smithii* available for this study seem to be slenderer than those of *G. chiragra;* this is borne out by the AWCLI for *smithii*, which ranges between 741 and 808, mean 769. This falls within the lower part of the range found for *G. chiragra*. The samples of both species are admittedly small.

The telson of *G. smithii* is usually longer than broad, although in some specimens length and width are subequal. The carinae of the telson may be slightly inflated in larger specimens, TL in excess of 65.0 mm, but these specimens can immediately be distinguished from *G. chiragra* by the evenly convex inner margin of the inner branch of the uropod.

G. smithii is not as broad as *G. platysoma*, and always has an anchor on the posterior portion of the median carina of the telson as well as distinct lateral teeth on the telson; in addition, *smithii* lacks the characteristic black dorsal spots of *G. platysoma*.

Serène (1954) recognized *G. smithii* from Viet Nam and suggested that *G. chiragra* var. *acutirostris* de Man was a synonym. This may be correct, but de Man's species differs in two important respects: (1) there are no tubercles on the anterior surface of the telson, and (2) the anchor is completely absent. The colour pattern of *G. acutirostris* (see Serène, 1947, p. 383) is very similar; the shape of the inner branch of the uropod is unknown. Until some specimens are found which show intergradation between these two species it seems best to recognize both.

Remarks.—The synonymy given above is undoubtedly incomplete, for most authors since Kemp (1913) have placed any and all variants under *G. chiragra*. As Kemp pointed out, Lanchester's *G. chiragra* var. D may be the same as *G. smithii*.

Distribution.—*G. smithii* is known with certainty only from Viet Nam (Serène, 1954), the Arafura Sea (Pocock, 1893), and from Arnhem Land and the Great Barrier Reef, Australia. The present questionable record from Bass Strait needs corroboration. Shallow water.

Gonodactylus chiragra (Fabricius, 1781)

Restricted synonymy:—

Gonodactylus chiragra; Fabricius, 1781, p. 515.—Kemp, 1913, p. 155, pl. IX, fig. 107, text-fig. 2 on p. 161.—Armstrong, 1941, p. 14.—Holthuis, 1941, p. 277, text-fig. 7.—Poisson, 1949, p. 23 [discussion; *chiraga*].—Tweedie, 1950, p. 139.—Barnard, 1950, p. 861.—Stephenson, 1952, p. 11; 1953, p. 47.—Dawydoff, 1952, p. 145.—Fourmanoir, 1953, p. 157, text-figs. 9-13 [development; possibly *G. platysoma*].—Holthuis, 1953, p. 61.—Tokioka, 1953, p. 127 [discussion]; 1953a, p. 143, text-fig. 1A.—Baig, 1954, p. 143 [listed].—Stephenson and McNeill, 1955, p. 250 [part].—Chuang, 1961, p. 180, pl. 80.—Stephenson, 1962, p. 34.—Manning, 1962, p. 3.

(*?*) *Gonodactylus chiragra chiragra:* Ingle, 1963, figs 27, 47, 63.

Material.—1 ♂, 50.9; north Australia; BM(NH) Reg. No. 58.97.—2 ♂, 74.0-78.2; Cape Borda, north-west Australia; Mrs B. Gray; BM(NH) Reg. No. 1932.11.30.185-186.—1 ♂, 78.0; reefs off S. entrance to Little Lagoon, Groote Eylandte, Arnhem Land, Northern Territory; Arnhem Land Expedition Sta. M48-9; 1948; USNM 111364.—1 ♂, 51.8; reef at Yirrkala, Arnhem Land, Northern Territory; Arnhem Land Expedition; 12th July, 1948; R. R. Miller and natives, col.; USNM 111369.—1 ♂, 14.5; reef at Yirrkala Mission, just NW of Cape Arnhem, Gulf of Carpentaria, Northern Territory; Arnhem Land Expedition Sta. C-2; 13th July, 1948; R. R. Miller, col.; AM.—1 ♂, 65.5; 1 ♀, 61.4; ironstone reef at rocky beach ca. 3 mi. S of the point E of Yirrkala and NW of Cape Arnhem, Northern Territory; Arnhem Land Expedition; 18th July, 1948; R. R. Miller and F. M. Setzler, col.; AM.—18 ♂, 28.8-79.6; 12 ♀, 36.0-71.2; ironstone reef (not coral) at Yirrkala, NW of Cape Arnhem, Northern Territory; Arnhem Land Expedition Sta. M48-21; emulsifiable rotenone; 6th August, 1948; R. R. Miller and natives, col.; AM (6 ♂, 6 ♀ to USNM 111363).—3 ♂, 66.2-78.0; 1 ♀, 63.0; reef at Yirrkala,

NW of Cape Arnhem; Northern Territory; Arnhem Land Expedition Sta. M48-21 (?); 12th August, 1948; R. R. Miller; USNM 111365.—1 ♀, 26.4; same; AM.—1 ♀, 13.5; coral reef at Yirrkala, NW of Cape Arnhem, Northern Territory; Arnhem Land Exped. Stats. C8-11; 25th August, 1948; R. R. Miller and natives, col.; AM.—2 ♂, 16.6-18.6; 2 ♀, 21.8-24.2; coral reef at Yirrkala, Arnhem Land, Northern Territory; Arnhem Land Exped. Stats. C13-17; 26th August, 1948; R. R. Miller, col.; USNM 111367.—9 ♂, 22.5-80.2; 12 ♀, 38.4-87.8 (in 7 lots); Great Barrier Reef, Queensland; British Great Barrier Reef Expedition, 1928-1929; BM(NH) Reg. No. 1937.9.21.414-4237.—1 ♀, 78.3; from coral crevices, North West Island, off Rockhampton, Queensland; *Endeavour* (*?*); AM Reg. No. E. 4504.—1 ♀, 57.0; Sydney, New South Wales; 21st March, 1948; F. D. McCarthy, col.; AM.—1 ♀, 63.5; same; USNM 111366.

Diagnosis.—Anterolateral angles of rostral plate rounded; eye-scales of moderate size, width usually greater than height, not extending laterally to edge of rostral plate; abdomen slender, AWCLI 756-855, mean 806 (n=26); carinae of sixth abdominal somite variously swollen and armed; carinae of telson variously swollen, rarely sharp, median usually lacking distal tubercle; anchor present; telson broader than long; marginal teeth of telson broad, lateral teeth present; inner branch of uropod tapering, inner margin sinuous, convex proximally, concave distally.

Colour.—Pattern almost completely faded in all of the present specimens; in the collection from Arnhem Land, all males have a darker ventral surface than females.

Size.—Males, TL 14.5-80.2; females, TL 13.5-87.8.

Discussion.—*G. chiragra*, as restricted here, can be distinguished from *G. platysoma* by the presence of lateral teeth on the telson, the narrower body, smaller eye-scales, lack of dark pigment patches on the body, and presence of an anchor on the telson. The sinuous inner margin of the uropodal inner branch distinguishes *chiragra* from the closely related *G. smithii*, which differs further in having sharp anterolateral angles on the rostral plate and a narrower telson usually ornamented with sharp, posteriorly-spined carinae.

The small specimens from Arnhem Land Expedition Sta. C13-17 appear to be adult in that the copulatory tubes of the males (TL 16.8-18.6 mm) are well developed and the carinae of the telson are very swollen. They also differ from the other available specimens in that the eye-scales are very small and erect, appearing taller than broad, and the anterolateral angles of the rostral plate are almost obtuse. The rostral plate is similar to that of *G. chiragra* var. *viridis* illustrated by Serène (1954). The telson of these small specimens is similar to that shown by Lanchester (1903) for G. *chiragra* var. *incipiens*. In view of the fact that there are only four specimens available and that nothing is known of their habitat or colour, it seems best to simply record them as variants. A revision of the genus may well show that they belong to a distinct species, corresponding to Kemp's dwarf races.

Remarks.—The specimen from the Red Sea illustrated by Ingle (1963) has sharp anterolateral angles on the rostral plate and may prove to be conspecific with *G. smithii*.

Distribution.—*G. chiragra* is widely distributed in the Indo-Pacific, from Japan, Oceania, and Australia to the Red Sea and South Africa. Stephenson and McNeill (1955) have summarized the numerous records from Australia. Shallow water.

Hadrosquilla, new genus

Definition.—Body depressed, compact; eyes small, cornea subglobular; rostral plate subquadrate; carapace narrowed anteriorly, smooth, without carinae, spines, or trace of cervical groove across dorsum; antennal protopod with 1 ventral and 2 mesial papillae; raptorial claw small, dactylus armed with 5-6 teeth; propodus stout, upper margin fully pectinate; propodi of third and fourth maxillipeds as broad as or broader than long; mandibular palp absent; 5 epipods present; thoracic and abdominal somites without longitudinal carinae, small spines present only at postero-lateral angles of sixth abdominal somite; telson broad, thick, with rounded dorsal median projection and irregularly sculptured area between dorsal projection and marginal armature which consists of, on either side of midline, (a) a row of fixed sub-median denticles, (b) 1 movable submedian tooth, (c) 2 intermediate denticles, (d) 1 intermediate tooth, (e) 1 lateral denticle, (f) 1 lateral tooth; basal prolongation of uropod produced into 2 trefoil spines, inner longer; inner branch of uropod with strong proximal fold on outer margin. Size small, TL 60 mm or less.

Type-species.—*Lysiosquilla perpasta* Hale, 1924. The genus is monotypic.

Gender.—Feminine.

Etymology.—The name is from the Greek, *hadros*, thick or bulky, in combination with the generic name *Squilla.*

Discussion.—*Hadrosquilla* most closely resembles *Nannosquilla*, particularly in the shape of the eyes, rostral plate, and inner branch of uropod, and in lacking a mandibular palp. It differs from *Nannosquilla* in having papillae on the antennal protopod, five epipods instead of four, in having a much stouter, more compact body, a stouter raptorial claw, with fewer teeth on the dactylus (5-6 instead of 7 or more), in having flattened spines on the basal prolongation of the uropod, in having only two intermediate denticles on the telson, and in lacking spatulate spines on the outer margin of the proximal segment of the uropodal outer branch, as well as lacking the long, ventrally-directed spinous process on the sixth abdominal somite in front of the articulation of each uropod. The rostral plate and eyes of *Hadrosquilla* also resemble those found in species of *Acanthosquilla*, but all members of that genus have five or more dorsal spines on the telson arranged in a semicircle.

Hadrosquilla differs from *Heterosquilla* in having elongate eyes with a subglobular cornea, a quadrate rather than cordiform or triangular rostral plate, a broad propodus on the raptorial claw, and a broad, triangular, ventrally-directed process on the sixth abdominal somite in front of the articulation of the uropod. The proximal fold on the inner branch of the uropod, among other features, distinguishes *Hadrosquilla* from the subgenera *Heterosquilla* and *Heterosquilloides* of *Heterosquilla*, and it shares this feature with the subgenus *Austrosquilla.* It can be distinguished from all the subgenera of *Heterosquilla* by the thick telson, with its broad, truncate median projection and highly sculptured posterior margin, which, as already noted, is similar to that found in *Nannosquilla.*

Hadrosquilla perpasta (Hale, 1924), new combination

Fig. 7

Lysiosquilla perpasta Hale, 1924, p. 497, pl. xxxiii, fig. 1, text-fig. 382.—Hale, 1927, p. 33, text-fig. 23; 1927a, p. 307 [listed].—Stephenson, 1952, p. 9; 1953; p. 45; 1955, p. 2.—Stephenson and McNeill, 1955, p. 245.

Heterosquilla perpasta: Manning, 1963, p. 321 [discussion].

Fig. 7.—*Hadrosquilla perpasta* (Hale), male, TL 30.3 mm, Moreton Bay. *a*, anterior portion of body; *b*, lateral processes of fifth, sixth, and seventh thoracic somites; *c*, ventral view of telson; *d*, basal prolongation of right uropod, ventral view; *e*, last abdominal somite, telson, and right uropod.

Material.—1 ♂, 34.2; Botany Bay, New South Wales; builds burrows amongst colonies of *Diopatra dentata* K.; between tides; exchange from M. Ward; USNM 78424.—1 ♂, 41.6; Kumell, Botany Bay, New South Wales; M. Ward; BM(NH) Reg. No. 1940.2.23.14.—1 ♂, 30.3; 1 ♀, 33.7; Dunwich, Stradbroke Is., Moreton Bay, Queensland; 19th July, 1952; R. Domrow, col.; exchange from Australian Museum; USNM 111355.

Description.—Eye small, cornea subglobular, set obliquely on stalk and overhanging it laterally; eyes not extending to end of antennular peduncle; eye-scales low, completely fused along midline.

Antennular peduncle short, less than half as long as carapace; dorsal processes of antennular somite produced into slender, anteriorly-directed spines, usually concealed by rostral plate.

Antennal scale small, less than one-third as long as carapace; antennal peduncle extending to cornea; antennal protopod with 1 ventral and 2 mesial papillae.

Rostral plate subquadrate, as broad as or broader than long, lateral margins convex; anterolateral angles acute; apex obtuse but sharp, slightly in advance of anterolateral angles.

Carapace short, small, narrowed anteriorly, without carinae or spines.

Dactylus of raptorial claw with 5-6 teeth, penultimate not shorter than antepenultimate; outer margin of dactylus evenly convex, with strong proximal notch, flanked proximally by a sharp lobe, distally by obtuse lobe; propodus short, stout, fully pectinate, with 4 movable spines, first longest, at base of inner margin; dorsal ridge of carpus terminating in sharp spine; merus stout, longer than ischium, inferodistal margin unarmed.

Propodi of third and fourth thoracic appendages beaded ventrally, broader than long, propodus of fourth twice as broad as that of fifth; propodus of fifth thoracic appendage as broad as long, with ventral brush of setae.

Mandibular palp absent; 5 epipods present.

Exposed thoracic somites smooth, straight or slightly rounded laterally; lateral portions of fifth somite concealed by carapace, but without conspicuous lateral process; basal segment of walking legs with blunt triangular process on posterior margin; inner branches of walking legs two-segmented, ovoid on first leg, elongate on third; eighth thoracic somite with low median ventral projection.

Abdomen smooth, compact, depressed, unarmed dorsally except for blunt posterolateral lobes on sixth somite; sixth somite with blunt ventral projection in front of each articulation of uropod.

Telson broad, convex, thick, with broad median dorsal projection, truncate posteriorly, with median notch; posterior margin of telson highly sculptured, with numerous projections above true posterior armature; "upper" armature consisting of, on either side of midline, a sharp or blunt lobe above movable submedian tooth, 3 variously shaped lobes between submedian and intermediate teeth, above intermediate denticles, and blunt submedian lobes and a blunt lobe above lateral denticle; marginal armature consisting of, on either side of midline, (a) 3-5 sharp submedian denticles, in a curved row, inner smallest and highest, (b) a sharp, movable submedian tooth, (c) 2 sharp intermediate denticles, (d) 1 fixed intermediate tooth, (e) 1 sharp lateral denticle, and (f) 1 broad lateral tooth.

Basal segment of uropod with sharp outer and dorsal carinae, dorsal extending to distal spine; proximal segment of outer branch shorter than distal, with 5-6 slender, movable spines on outer margin, last extending slightly beyond midpoint of distal segment; distal angle of proximal segment of outer branch with broad rounded lobe armed with 5-6 stiff setae; inner branch elongate, tapering, proximal portion of outer edge folded over; basal prolongation consisting of 2 flattened spines, carinate ventrally, inner longer.

Colour.—Background cream, entire surface of body covered with small, stellate, black chromatophores, aggregated into long, broad bar on last 3 thoracic and first 5 abdominal somites; carapace also with 1 pair of anterior black spots along gastric grooves, 3 spots, 1 mesial, 2 lateral, in area of cervical groove, and 1 on median posterior margin.

Measurements.—Males, TL 15-45 mm; females, TL 21-55 mm (Stephenson and McNeill, 1955). Other measurements, in mm, of male, TL 34.2 mm: carapace length, 6.6; cornea width, 1.0; rostral plate length, width, 2.1, 2.2; fifth abdominal somite width, 6.8; telson length, width, 3.3, 5.5.

Discussion.—The thick telson with its highly sculptured posterior margin is characteristic of this species, and that feature, in combination with the small number of teeth on the claw (5-6), the compact body and the presence of only two intermediate denticles on the telson will distinguish it from similar species in *Heterosquilla* and *Nannosquilla.*

Distribution.—South-eastern coast of Australia, where it has been recorded from Queensland, New South Wales, Victoria, and South Australia. Stephenson (1955) also recorded it from Tasmania. Subtidal to 10 m.

Heterosquilla Manning, 1963

Heterosquilla Manning, 1963, p. 320.

Definition.—Body depressed, compact; eyes of moderate size, cornea usually bilobed or expanded; rostral plate usually triangular or cordiform; antennal protopod with one or more papillae; carapace narrowed anteriorly, smooth, without trace of carinae, spines, or cervical groove across dorsum; raptorial claw large, dactylus armed with 4 or more teeth; propodus slender, fully pectinate; mandibular palp usually present; at least 4 epipods present; thoracic and abdominal somites without longitudinal carinae, sixth somite with posterolateral spines and with or without additional dorsal spines; telson broad, with variously shaped median dorsal projection and with or without additional submedian dorsal projections or spines; marginal armature of telson consisting of, on either side of midline, (a) a row of submedian denticles, (b) 1 movable submedian tooth, (c) 2 or 4 intermediate denticles, (d) 1 intermediate tooth, (e) 1 lateral denticle, and (f) 1 lateral tooth; basal prolongation of uropod produced into triangular spines, length variable; inner branch of uropod usually without strong proximal fold on outer margin. Size moderate, maximum TL about 100 mm.

Remarks.—Thirteen species were provisionally referred to this genus when it was originally diagnosed (Manning, 1963). At that time I noted that the genus probably included several unrelated groups. Since 1963, studies have shown that two species, *Squilla eusebia* Risso and *Lysiosquilla enodis* Manning, are quite distinct from the remainder of the species in *Heterosquilla*, and these will be referred to a new genus in a revision of the Western Atlantic stomatopods now nearing completion. A study of the Australian species which were not available when the preliminary revision of *Lysiosquilla* was published indicates that one new genus and two new subgenera should now be proposed.

As shown below, two other species originally referred to *Heterosquilla*, *H. latifrons* (de Haan) and *H. spinosa* (Wood-Mason), are each made up of two closely-related but distinct species. *H. brazieri* (Miers) is the Australian analogue of the Japanese *H. latifrons; H. brazieri* was recently resurrected as a subspecies of *H. latifrons* by Stephenson (1962), but a direct comparison of specimens of both species leaves little doubt that they are distinct. Also, *H. tricarinata* (Claus) from New Zealand is distinct from *H. spinosa* (Wood-Mason) from the Andaman Islands; both species had previously been referred to *H. spinosa.*

H. perpasta (Hale) is here referred to a new genus. As noted in the discussion of that genus, it differs in many respects from the other species now placed in *Heterosquilla* and seems to be more closely related to *Nannosquilla* than *Heterosquilla.*

The twelve remaining species of *Heterosquilla* fall into two distinct groups, with either two or four intermediate marginal denticles present on the telson. There are four species in the former group, two from South America, *H. platensis* (Berg) (the type-species) and *H. polydactyla* (von Martens), and two from the Indo-Pacific, *H. tricarinata* (Claus) and *H. spinosa* (Wood-Mason). All share the following features: (1) the outer spine of the basal prolongation of the uropod is much larger than the inner; (2) there is no strong fold on the proximal portion of the outer margin of the uropodal inner branch; (3) the inner branches on the walking legs are slender; and (4) the rostral plate is cordiform. The cornea of the two American species is broadened, almost bilobed, whereas that of the Indo-Pacific species is subglobular. These four southern species are placed in the nominate subgenus, *Heterosquilla*.

The remaining eight species, all of which have four intermediate marginal denticles on the telson, also fall into two distinct groups. The two Australian species, *H. osculans* (Hale) and *H. vercoi* (Hale), differ from all the remainder in three features. The eye is subglobular and set very obliquely on the stalk (as in *Nannosquilla*), there is a strong fold on the inner margin of the uropodal inner branch, and there is a strong inferodistal spine on the ischium of the raptorial claw. These two species are referred to a new subgenus, *Austrosquilla*.

The remaining six species of *Heterosquilla* are very similar morphologically. All but the east American *H. armata* (Smith) have the inner spine of the basal prolongation of the uropod longer than the outer. All have a broad eye, with a bilobed cornea, a triangular rostral plate, and a slender inner branch on the uropod, lacking a strong proximal fold. These six species are referred to a second new subgenus, *Heterosquilloides*.

KEY TO INDO-PACIFIC SPECIES OF HETEROSQUILLA

1. Two intermediate marginal denticles present on telson. Subgenus *Heterosquilla* 2
   Four intermediate marginal denticles present on telson..... 3
2. Basal prolongation of uropod with distinct inner spine .... *tricarinata*, p. 120
   Basal prolongation of uropod with at most a rounded lobe ..... [*H. spinosa* (Wood-Mason, 1895)]
3. Ischium of raptorial claw unarmed; cornea expanded, usually bilobed; proximal portion of inner branch of uropod without strong fold. Subgenus *Heterosquilloides* 4
   Ischium of raptorial claw with inferodistal spine; cornea subglobular; proximal portion of outer margin of uropodal inner branch strongly folded over. Subgenus *Austrosquilla* 6
4. Ventral surface of telson with strong postanal spine; sixth abdominal somite armed as posterolateral angles only..... 5
   Ventral surface telson without postanal spine; sixth abdominal somite with dorsal spines in addition to those at posterolateral angles ..... [*H. insignis* (Kemp, 1911)]
5. One or more short longitudinal carinae present between median projection and anteriorly-connected submedian dorsal carinae..... *brazieri*, p. 125
   No short carinae present between median and anteriorly-connected submedian dorsal carinae ..... [*H. latifrons* (de Haan, 1844)]
6. Dorsal projection of telson spinous; rostral plate subquadrate.....*osculans*, p. 127
   Dorsal projection of telson obtuse, blunt; rostral plate triangular....*vercoi*, p. 130

Heterosquilla (Heterosquilla) tricarinata (Claus, 1871)

Fig. 8

Coronis tricarinata White, 1847, p. 85 [*nomen nudum*].

Coronis tricarinata Claus, 1871, p. 21.

Coronis spinosa Wood-Mason, 1875, p. 232; 1876, p. 263 [part].

Squilla indefensa Kirk, 1878, p. 466; 1879, p. 394, text-fig. on p. 394; 1879a, p. 401.—Filhol, 1885, p. 52 [listed]; 1886, p. 436, pl. 53, fig. 3.—Bigelow, 1894, p. 503 [key only].

Squilla laevis Hutton, 1879, p. 340.—Filhol, 1886, p. 491.—Bigelow, 1894, p. 503 [key only] [not *S. laevis* Hess, 1865].

Lysisosquilla spinosa: Miers, 1880, pp. 12, 125, pl. 1, figs 10-12.—Chilton, 1891, pp. 61, 63, pl. 10, figs 1-3.—Bigelow, 1894, p. 503 [key only].—Wood-Mason, 1895, p. 1, pl. 1, figs 1-3 [part; reference to New Zealand specimens only].—Hutton, 1904, p. 256 [listed].—Chilton, 1906, p. 270 [listed]; 1909, p. 615 [listed]; 1911, p. 139, text-fig. 4; 1911a, p. 306.—Thomson, 1913, p. 241 [listed].—Kemp, 1913, p. 118, pl. 8, fig. 94 [part; reference to New Zealand specimen only].—Thomson and Anderton, 1921, p. 108.—Young, 1929, p. 154 [listed].—Powell, 1947, p. 37.—Ralph and Yaldwyn, 1956, p. 64, pl. I, fig. 5.

not *Squilla tridentata* Thomson, 1882, p. 230.—Bigelow, 1894, p. 503 [key only].

not *Lysiosquilla spinosa:* Lanchester, 1901, p. 554.

Material.—1 ♂, 68.8; 1 ♀, 61.7; dug from sandflats, Portobello, Otago Harbour, New Zealand; 12th November, 1952; J. C. Yaldwyn, col.; exchange from Australian Museum; USNM 111358.—1 ♂, 77.5; Parakanui, Otago, New Zealand; from Otago University Museum; BM(NH) Reg. No. 86.56.—2 ♂, 50.5-67.2; Stewart Is., nr. New Zealand; A. Lysaght, pres.; BM(NH) Reg. No. 1955.10.20.6/7.—1 ♂, 54.3; Stewart [Is. (?)]; Filhol, col.; MNHNP.—1 dry ♂, CL 6.6; no specific locality; Ross Antarctic Exped., col.; holotype; BM(NH).

Description.—Eye small, cornea subglobular, set obliquely on stalk; ventral margin of stalk with prominent projecting lobe; eyes extending slightly beyond end of second segment of antennular peduncle; eye-scales erect, completely fused along midline.

Antennular peduncle short, about one-third as long as carapace; basal segment with proximal spine and 2 fleshy lateral papillae; dorsal processes of antennular somite produced into triangular lobes directed anterolaterally, visible either side of rostral plate.

Antennal scale small, less than half as long as carapace; antennal peduncle extending to end of cornea; antennal protopod with 2 ventral papillae.

Rostral plate triangular or cordiform, broader than long, anterolateral margins tapering to acute but blunt apex which extends to proximal portion of eyes.

Carapace smooth, short, narrowed anteriorly, without carinae or spines.

Dactylus of raptorial claw with 9-13 teeth, penultimate not markedly shorter than antepenultimate; outer margin of dactylus sinuate, with basal notch; propodus fully pectinate, with 3 movable spines at base, proximal the largest; dorsal ridge of carpus terminating in sharp tooth; merus longer than ischium, outer inferior angle unarmed; basis with ventrally-projecting tooth on inner margin.

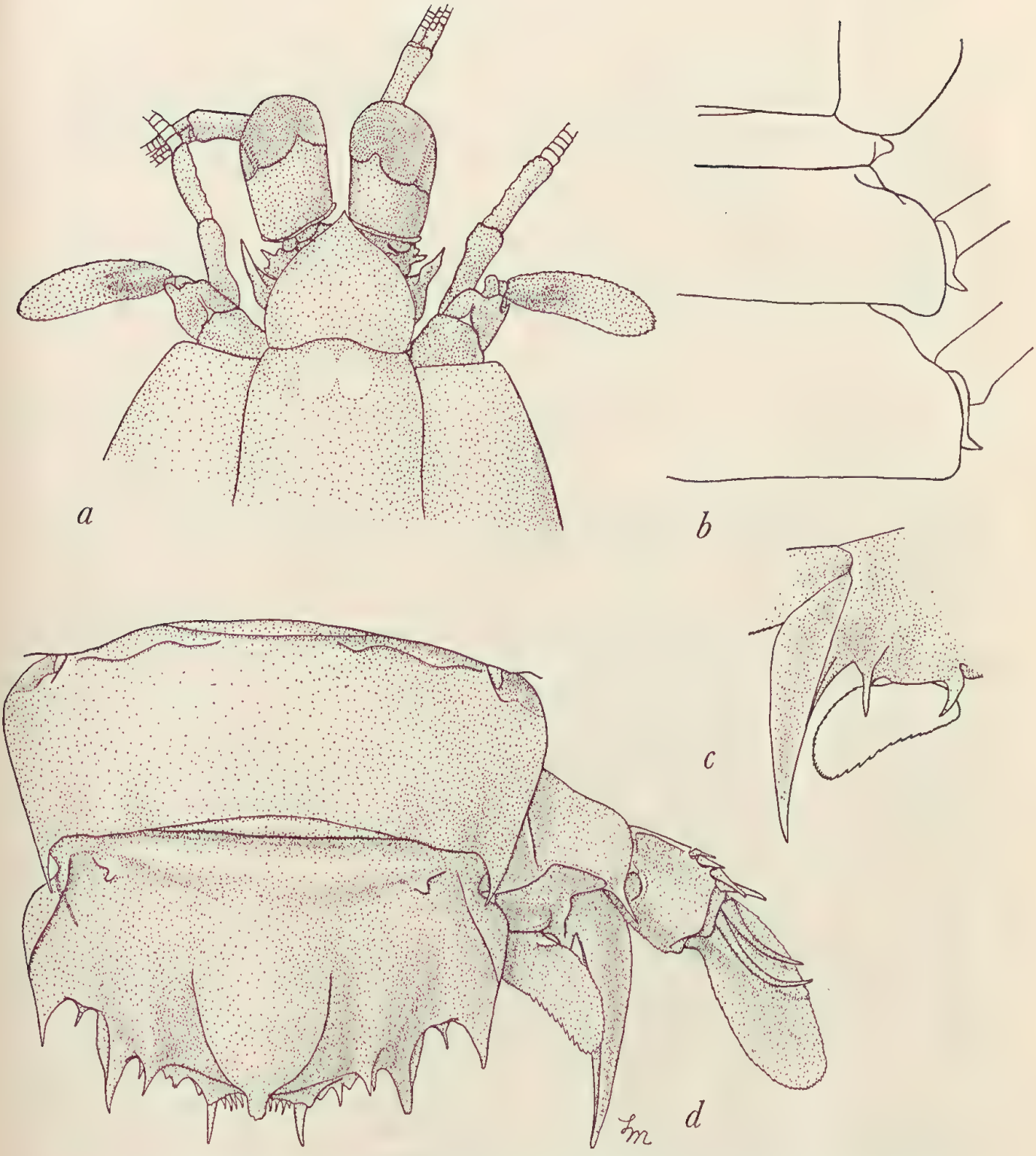

Fig. 8.—*Heterosquilla* (*Heterosquilla*) *tricarinata* (Claus), female, TL 61.7 mm, Otago Harbour. *a*, eye; *b*, lateral processes of fifth, sixth, and seventh thoracic somites; *c*, basal prolongation of right uropod, ventral view; *d*, sixth abdominal somite, telson, and right uropod.

Propodus of third and fourth thoracic appendages each beaded ventrally broader than long, propodus of fourth twice as broad as that of fifth appendage; propodus of fifth appendage as broad as long, with ventral brush of setae.

Mandibular palp present; 5 epipods present.

Exposed thoracic somites smooth dorsally; fifth somite with thin, blade-like, ventrally-directed lateral process, usually appearing acute in dorsal view, rounded ventrally; lateral processes of next 2 somites convex laterally, rounded anteriorly, more truncate posteriorly; basal segments of walking legs with large triangular outer spine and small sharp inner spine on posterior margin; inner branches of walking legs ovate on first 2 legs, elongate on third, two-segmented; eighth thoracic somite with low median ventral keel.

Abdomen smooth, depressed, usually armed at posterolateral angles of sixth somite only, posterolateral angles of fifth somite rarely armed; sixth somite with longitudinal lateral grooves, not sharply defined, and ventral projection in front of articulation of each uropod; sixth somite with slight median projection on postero-ventral margin in male, female with posterolateral projections, armed with spinules on one side; anterolateral plates fully articulated.

Telson broad, with broad median dorsal elevation, tipped with rounded or blunted lobe, and 2 low submedian elevations, each terminating in sharp tooth; 3 pairs of marginal teeth, movable submedians, fixed intermediates and laterals, with intervening denticles, arranged as follows: submedian, 6-10; intermediate, 2; lateral, 1; submedians in convex row on each side; low lobe present between sub-median tooth and first intermediate denticle, second low lobe between each inter-mediate denticle; oblique lateral carinae and anterolateral tubercles also present on dorsal surface.

Basal segment of uropod with sharp dorsal carina, extending almost to distal spine before curving ventrally; proximal segment of outer branch with 5-6 slender spines, last 2 elongate, strongly recurved, extending past midpoint of distal segment; inner distal angles of proximal segment of outer branch with rounded lobe, armed with 6-9 stiff setae; distal segment of outer branch longer than proximal; inner branch short, stout, convex, proximal portion of outer margin lacking strong fold; basal prolongation flattened, outer spine with strong ventral carina, much larger than inner spine; slender proximal spine also present on basal prolongation at articulation of inner branch.

Colour.—Male with 2-3 transverse bars of dark pigment on each body segment, anterior diffuse, posterior sharply defined, posterior not extending to ventral margin of pleuron; female with most of body dark, each segment with median and posterior clear areas; both sexes with 2 broad, submedian black patches on telson, interrupted by clear longitudinal line along midline, between median elevation and submedians, and along submedian elevations; uropod with broad proximal and distal dark patches, separated by clear area. The colour of living animals has been recorded by Chilton (1891) and Ralph and Yaldwyn (1956).

Measurements.—Males, TL 50.5-77.5 mm; female, TL 61.7 mm. Other measurements of 68.8 mm male, in mm: carapace length, 13.2; cornea width, 2.5; rostral plate length, width, 3.2, 3.7; fifth abdominal somite width, 14.4; telson length, width, 6.8, 11.5.

Discussion.—Although the forms originally recorded from New Zealand and the Andamans by Wood-Mason have always been considered to be conspecific, in my opinion the two should be considered distinct. The New Zealand species, herein referred to *H. tricarinata*, differs from the species recorded from the Andamans (and

perhaps Penang, Malaya) in several minute but important points, as follows: (1) in *H. spinosa* the basal segment of each walking leg is armed with one spine, whereas in *H. tricarinata* there are two; (2) *H. spinosa* has three sharp dorsal spines, the median of which, according to Kemp (1913), is situated on a conspicuous lobe; in *H. tricarinata* only the two lateral spines are sharp, the median (at least in the specimens reported herein) is bluntly rounded posteriorly and is situated on a prominent, elevated projection, almost carinate laterally; (3) *H. spinosa* lacks an inner spine on the basal prolongation of the uropod; this spine is well-developed in *H. tricarinata*. The most important difference between the two species is the lack of the inner spine on the basal prolongation of the uropod in *H. spinosa* and its presence in *H. tricarinata*. A direct comparison of specimens of both species might well show other differences.

H. tricarinata was first used by White (1847) in his List of the Crustacea of the British Museum; the name was merely listed and not described, and has been considered as an unidentifiable *nomen nudum*. White's specimen was later examined by Claus, who validated the name in his classic paper on stomatopod larvae published in 1871; Claus included remarks on some of the characters of White's specimen. Claus's use of the name would probably have been overlooked by me if it had not been brought to my attention by L. B. Holthuis.

While at the British Museum in June, 1964, I had the opportunity of examining White's specimen and I was able to verify that it belongs to this common species from New Zealand, as suggested by Miers (1880).

Coronis spinosa Wood-Mason, which is here restricted to the species reported from the Andaman Islands (Wood-Mason, 1875) and Penang, Malaya (Lanchester, 1901), was originally described from two females, one from the Andaman Islands, the other from New Zealand. No type was designated originally by Wood-Mason, but Kemp (1913, p. 120) selected the female from Port Blair, Andamans as the type. The name *spinosa* can be used for the more northern form, *tricarinata* for the species in New Zealand. If they prove to be conspecific, the older name, *tricarinata*, must be used. To my knowledge, only Wood-Mason (1875, 1876, 1895), Lanchester (1901), and Kemp (1913) actually deal with *H. spinosa* s.s.; specimens reported as *Coronis spinosa* or *Lysiosquilla spinosa* by all other authors are probably referable to *H. tricarinata*.

I follow Chilton (1891) and Kemp (1913) in synonymizing *Squilla laevis* Hutton and *Squilla indefensa* Kirk with *H. tricarinata*. I do not agree that *Squilla tridentata* Thomson, which has but four teeth on the dactylus of the raptorial claw, is conspecific with *H. tricarinata*, which has 9-11 teeth on the claw. Thomson's specimen is obviously a juvenile or post larva, and the armature of the raptorial claw is one feature that is not known to change with age. Thomson's type, if extant, should be re-examined and redescribed.

H. tricarinata is very similar to the American *Heterosquilla platensis* (Berg) from Argentina. Although agreeing with *H. platensis* in general appearance, *H. tricarinata* differs as follows: (1) the eye of *tricarinata* is smaller, with the cornea less expanded; (2) the apex of the rostral plate is shorter, and the anterolateral angles are not as strongly concave; (3) the antennal scale is not as elongate or slender; (4) there are 9-12 teeth on the claw of *tricarinata*, 13-15 in *platensis;* (5) the basal spines of the walking legs are more prominent in *tricarinata;* (6) *platensis* has 9-13 submedian denticles in a transverse row on the telson, *tricarinata* has 12-19 in two curved rows; (7) the submedian dorsal carinae of the telson are poorly marked in *tricarinata*, very prominent in *platensis;* (8) the lateral longitudinal carinae of the sixth abdominal somite are much more prominent in *platensis* than in *tricarinata;* (9) the inner spine of the basal prolongation is comparatively smaller in *tricarinata;* (10) the inner branch of the uropod is much longer and slenderer in *platensis* than *tricarinata*. In general colour pattern the two species are very similar; in *platensis* there is no colour

dimorphism, and both sexes resemble the males of *tricarinata*. There are some minor colour differences, such as the absence of a dark encircling ring on the antennal scale of *tricarinata*.

H. tricarinata also resembles the American *H. polydactyla* (von Martens), but the latter is immediately distinguished by its long rostral plate and large (17-20) number of teeth on the dactylus of the raptorial claw.

Remarks.—According to Article 23(b) of the present International Code of Zoological Nomenclature, *Coronis tricarinata* Claus must be considered as a *nomen oblitum*, since it has not been used in over 50 years. Since the International Commission itself has not been able to interpret this rule, which does systematics a gross disservice by unnecessarily multiplying names and by circumventing the Law of Priority, Claus's name is used here. There is no good reason for not using *C. tricarinata* for this species and there are numerous good reasons for not introducing a new name here. *Coronis tricarinata* Claus is the oldest name for the species and should be used.

Distribution.—*H. tricarinata* is known only from the waters of New Zealand and some surrounding islands. Records in the literature are: Hobson Bay and St Helier's Bay, Auckland Harbour; Kapiti Island and Waikanae, Wellington; Otago Harbour, Dunedin, and Resolution Island, Dusky Sound, Southland; Stewart Island; Chatham Islands; Auckland Islands. Known intertidally but bathymetric range has not been recorded.

Heterosquilloides, new subgenus

Diagnosis.—Cornea large, bilobed; rostral plate triangular or sub-cordiform; ischium of raptorial claw without inferodistal spine; 4 intermediate denticles on telson; inner branch of uropod without strong proximal fold on outer margin; inner spine of basal prolongation of uropod usually the longer.

Type-species.—*Lysiosquilla insolita* Manning, 1963.

Gender.—Feminine.

Etymology.—The name is composed of the Latin suffix, *—oides*, in combination with the generic name *Heterosquilla*.

Discussion.—This subgenus includes six of the species originally assigned to *Heterosquilla*, *H. latifrons* (de Haan), *H. brazieri* (Miers), *H. armata* (Smith), *H. insignis* (Kemp), *H. mccullochae* (Schmitt), and *H. insolita* (Manning). The bilobed cornea and the presence of four intermediate denticles on the telson will distinguish members of this subgenus from those in the nominate subgenus which have a broadened eye and but two intermediate denticles. As in the nominate subgenus, the inner branch of the last walking leg of *Heterosquilloides* is very slender and there is no strong fold on the inner, proximal margin of the uropodal inner branch. Species of this subgenus all have a very ornate telson, with the broad median elevation flanked by several variously armed carinae. Of the species assigned here, only *H. armata* has the outer spine of the uropodal basal prolongation longer than the inner.

The more ornate telson, with more than one dorsal spine, and the lack of the inferodistal spine on the ischium of the claw, among other features, will distinguish members of this subgenus from the third subgenus, *Austrosquilla*.

Heterosquilla (Heterosquilloides) brazieri (Miers, 1880)

Lysiosquilla Brazieri Miers, 1880, pp. 11, 125, pl. I, figs 3-6.—Haswell, 1882, p. 206.—Whitelegge, 1889, p. 222.—Bigelow, 1894, p. 503 [key only].—Chilton, 1911, p. 139.

Lysiosquilla latifrons: Kemp, 1913, p. 128 [part].—Stephenson and McNeill, 1955, p. 248 [not *L. latifrons* de Haan, 1844].

Lysiosquilla latifrons brazieri: Stephenson, 1962, p. 38, pl. I, figs A-D, text-figs 1e-1f.

Material.—1 ♀, 99.0; Port Jackson, New South Wales; J. Brazier; holotype; BM(NH) Reg. No. 79.8.—1 ♀, 56.3; trawled off Kingscliff, New South Wales; 56 m; June, 1961; L. Wale, col.; AM Reg. No. P. 13767.

Description.—Eye of moderate size, cornea bilobed, with prominent mesial tubercle; eye-scales erect, separate; eyes extending beyond end of first segment of antennular peduncle.

Antennular peduncle short, slightly more than half as long as carapace; dorsal processes of antennular somite visible lateral to rostral plate as erect spines, apex curved anteriorly.

Antennal protopod with at most 1 ventral papilla; antennal peduncle, long, extending well beyond eye; antennal scale more than one-third as long as carapace.

Rostral plate short, much broader than long; basal portion very short, broadly rounded laterally, apical spine long; apical spine bifurcate in dorsoventral plane, ventral spine fitting between eye-scales.

Carapace short, strongly narrowed anteriorly, with rounded anterolateral angles and more broadly rounded posterolateral angles.

Raptorial claws missing in Kingscliff specimen; dactylus in type armed with 6 teeth.

Propodus of third thoracic appendage broader than long, beaded ventrally; fourth thoracic appendages missing in Kingscliff specimen; propodus of fifth thoracic appendage as broad as long, with ventral brush of setae.

Exposed thoracic somites smooth dorsally, fifth without conspicuous lateral or ventral processes; lateral processes of sixth and seventh somites rounded, lateral process of sixth somite smaller than that of seventh, on both somites processes anteriorly rounded, posteriorly angled, apex rounded; basal segments of walking legs each with single posterior spine; inner branches of walking legs two-segmented, ovate on first 2 legs, slender on last; low median ventral projection present on eighth thoracic somite.

Abdomen compact, depressed, smooth, armed only at posterolateral angles of sixth somite; sixth somite also with lateral, longitudinal grooves, sharply defined mesially, parallel to lateral margin; ventrolateral spine present on each side of sixth somite in front of articulation of uropod.

Telson broad, with broad, sharply-defined median elevation terminating in 3 sharp spines; dorsal armature consisting of median elevation and 3 pairs of dorsal carinae; each armed posteriorly; median elevation connected anteriorly with second submedian carina on each side, first submedian carina lying in well-defined submedian depression; type with 2 carinae in depression; outer dorsal carina not as sharply defined dorsally as remainder; lateral carinae also present dorsally; anterior surface of telson with 1 pair of sharp, erect tubercles; posterior spinules, variable in number and position, present between apical spines of dorsal carinae and marginal armature;

posterior margin with shallow median sinus and, on either side of midline, (a) a curved row of 8-10 slender submedian denticles, (b) 1 short, movable submedian tooth, (c) 4 intermediate denticles, second and fourth slenderest and sharpest, (d) 1 intermediate tooth, (e) 1 lateral denticle, and (f) 1 lateral tooth; ventral surface with strong postanal spine.

Basal segment of uropod with strong dorsal carina extending to distal spine; proximal segment of outer branch shorter than distal, with 6 sharp spines on outer margin, distal 2 curved, distal extending well past midpoint of ultimate segment; proximal segment with 8-9 stiff setae on inner, distal lobe; inner branch broad, curved, proximal portion of outer margin with slight fold; spines of basal prolongation flattened, strongly carinate ventrally, inner longer; smaller, ventral spine present at articulation of inner branch.

Colour.—Rostral plate and anterior appendages with patches of dark pigment; carapace with at least 2, possibly 3, bands of dark pigment, increasing posteriorly in size and intensity of colour, posterolateral angles darkest (anterior bar poorly defined in Kingscliff specimen), several darker spots present on each bar; exposed thoracic and first 5 abdominal somites with 2 dark bands, anterior diffuse, posterior darker, more sharply-defined; anterolateral plates of abdomen black, adjacent areas on first abdominal somite darker than most of remainder of body; posterolateral angles of fifth abdominal somite very dark, with short, oblique, clear stripe; telson pattern varied, median elevation dark but with clear midline, 2 broad dark areas also present; outer branch of uropod with distal half of proximal segment and proximal half of distal segment dark; inner branch of uropod dark, with clear midline.

Measurements.—Females only examined, TL 56.3-99.0 mm; other measurements of 56.3 mm female, in mm: carapace length, 11.2; cornea width, 2.7; rostral plate length, width, 2.5, 3.8; fifth abdominal somite width, 12.7; telson length, width, 5.8, 10.7.

Discussion.—Chilton (1911) suggested that *L. brazieri* was identical with *L. latifrons* and Kemp (1913) agreed and synonymized the two. As both Kemp and Stephenson (1962), who regarded *brazieri* as a subspecies of *latifrons*, pointed out, the main differences originally pointed out by Miers (1880) were invalid; Miers used the following characters: (1) *brazieri* had six teeth on the claw instead of seven; (2) *brazieri* had more submedian marginal denticles than *latifrons* and lacked a median sinus on the telson; and (3) *brazieri* had slender inner branches on the last walking legs. I agree with Stephenson that these are not valid diagnostic characters inasmuch as there is considerable overlap in them between specimens from Japan and those from Australia, but a comparison of specimens from each locality shows that there are constant differences in other features.

The two specimens of *H. latifrons* listed by Holthuis (1941) were examined during a recent visit to the Leiden Museum; as Holthuis noted, one of these specimens is probably de Haan's (1844) type. A third specimen, that reported by Rathbun (1902), was compared with de Haan's specimens as well as the specimen from Kingscliff upon which this description is based. De Haan's specimens have but six teeth on the claw, as in *brazieri*, and have 10-12 submedian denticles; *brazieri* has 8-10, so there is some degree of overlap. Specimens of both species have a shallow median sinus on the telson and a slender inner branch on the last walking leg.

The most important difference between the species, and one which could not be detected from published illustrations of *latifrons*, is the dorsal armature of the telson. In *H. brazieri* there are one or more sharp carinae lying in the broad, dorsal depression that is situated lateral to the median elevation; these carinae are absent in *H. latifrons*. *H. brazieri* also differs from *latifrons* in having from 2-11 spinules on

the posterior margin between the dorsal spines and the marginal spines; these spinules are absent in *latifrons*. Finally, *brazieri* has a prominent tubercle on the mesial portion of the cornea which is absent in *latifrons*. In my opinion *latifrons* and *brazieri* must be considered as two distinct species.

Both *latifrons* and *brazieri* are also related to the American *H. mccullochae* (Schmitt), but that species has only 4 teeth on the claw and lacks the strong postanal spine present in its Indo-Pacific counterparts.

The strong postanal spine and the bifurcate rostral spine in *latifrons* and *brazieri* will distinguish them from all other Indo-Pacific species of *Heterosquilla*.

Remarks.—Stephenson (1962) has illustrated this species, so no figures are provided here. *H. latifrons* should be redescribed and illustrated in detail.

Although Stephenson (1962) noted that there might be some colour differences between *H. brazieri* and *H. latifrons*, these are not evident in the present material, as the pattern is at least partially faded. Comparison of recently-collected specimens of both species might well reveal differences in colour pattern.

Distribution.—Four specimens of *H. brazieri* are known from Australia, from New South Wales and the New South Wales-Queensland border, in moderate depths, 60 m or less; an additional two specimens have been collected from Otaki, New Zealand. *H. latifrons* is known only from Japan.

Austrosquilla, new subgenus

Diagnosis.—Cornea subglobular; rostral plate either triangular or subquadrate; ischium of raptorial claw with strong inferodistal spine; 4 intermediate denticles on telson; inner branch of uropod with strong proximal fold on outer margin; basal prolongation of uropod with inner spine longer.

Type-species.—*Lysiosquilla vercoi* Hale, 1924.

Gender.—Feminine.

Etymology.—The name is from the Latin, *australis*, southern, in combination with the generic name *Squilla*.

Discussion.—The subgenus *Austrosquilla* of *Heterosquilla* includes two species known only from Australia, *Lysiosquilla vercoi* Hale and *L. osculans* Hale, both of which are redescribed below. Whereas this subgenus shares many features with the subgenera *Heterosquilla* and *Heterosquilloides*, it also exhibits some characters more typical of *Acanthosquilla* and *Nannosquilla*, especially the shape of the eye and the presence of a strong fold on the proximal outer margin of the uropodal inner branch. Also the strong, ventrally-directed process which has on the sixth abdominal somite in *Acanthosquilla* and *Nannosquilla*, is reduced to a small spine in *Austrosquilla;* in *Heterosquilla* and *Heterosquilloides* this process is reduced to a blunt posterolateral projection. Finally, the inner branches of the walking legs are more ovate than in either of the other two subgenera of *Heterosquilla*. It seems possible that *Austrosquilla* should be considered as a distinct genus.

Heterosquilla (**Austrosquilla**) **osculans** (Hale, 1924)

Fig. 9

Lysiosquilla vercoi var. *osculans* Hale, 1924, p. 501, pl. xxxiii, fig. 3, text-fig. 384.

Lysiosquilla osculans: Hale, 1927, p. 34, text.fig. 25.—Stephenson and McNeill, 1955, p. 247.—Stephenson, 1955, p. 3; 1962, p. 34.

Heterosquilla osculans: Manning, 1963, p. 321 [listed; discussion].

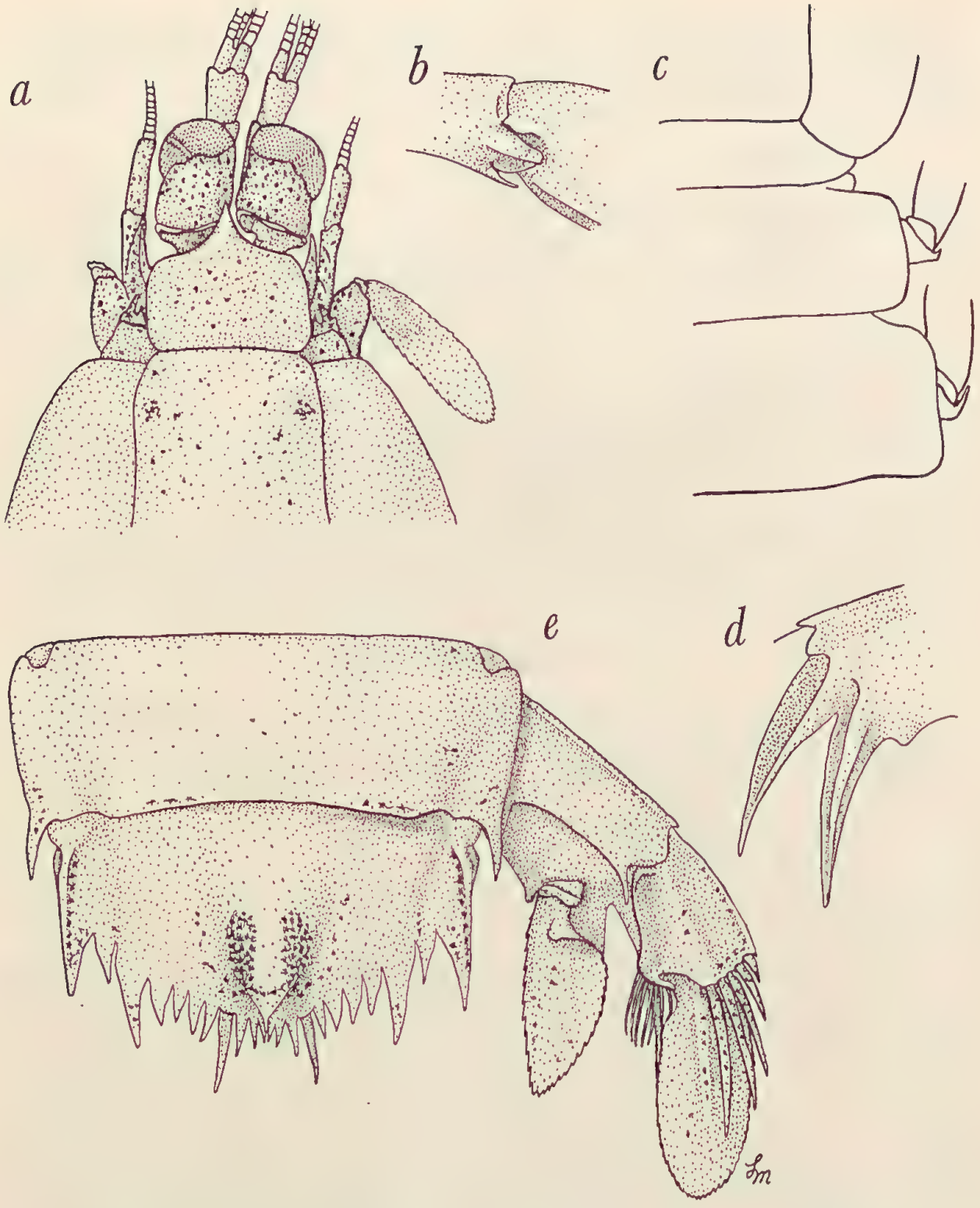

Fig. 9.—*Heterosquilla* (*Austrosquilla*) *osculans* (Hale), male, TL 42.7 mm, Beaumaris. *a*, anterior portion of body; *b*, ischiomeral articulation of raptorial claw; *c*, lateral processes of fifth, sixth, and seventh thoracic somites; *d*, basal prolongation of right uropod, ventral view; *e*, sixth abdominal somite, telson, and right uropod.

Material.—1 ♂, 42.7; Beaumaris, Port Phillip, Victoria; January, 1926; M. Ward, pres.; AM Reg. No. P. 8606.

Description.—Eye small, cornea subglobular, set obliquely on stalk and slightly overhanging stalk laterally; lateral margin of stalk with rounded prominence; eyes extending slightly beyond end of second segment of antennular peduncle; eyes-scales small, erect, fused along midline.

Antennular peduncle short, less than half as long as carapace; dorsal processes of antennular somite visible as sharp, anteriorly-directed spines lateral to rostral plate.

Antennal scale small, about one-third as long as carapace; antennal protopod with 1 ventral and 2 mesial papillae.

Rostral plate quadrangular, broader than long, with rounded anterolateral angles and sharp anterior spine.

Carapace smooth, narrowed anteriorly, without carinae or spines.

Dactylus of raptorial claw with 9 teeth, antepenultimate slightly but not markedly shorter than distal; outer margin of dactylus evenly curved with sharp basal denticle flanked distally by shallow groove; propodus stout, fully pectinate, with 4 movable teeth at base, proximal the longest; carpus with sharp dorsal carina terminating in strong tooth; ischium elongate but shorter than merus, with sharp subdistal spine at end of prominent ventral carina.

Propodi of third and fourth thoracic appendages beaded ventrally, as broad as or broader than long, propodus of fourth broader than that of third appendage and over twice as broad as that of fifth; propodus of fifth appendage as broad as long, with ventral brush of setae.

Mandibular palp absent; 4 epipods present.

Fifth thoracic somite without prominent lateral process or ventral spines; lateral processes of next two somites truncate, rounded anterolaterally and posterolaterally; basal segments of first 2 walking legs with inner and outer spines (appearing sharp in dorsal view, actually triangular), last leg in male with outer spine only; eighth thoracic somite with low triangular prominence on ventral surface.

Abdomen smooth, depressed, without dorsal carinae, armed only at posterolateral angles of last somite; anterolateral plates fully articulated; sixth somite with triangular ventral spine in front of articulation of each uropod.

Telson broad, flattened, with low median prominence terminating in sharp posterior spine; posterior armature of telson consisting of, on either side of midline, (a) 3 graded submedian denticles, outer largest, (b) a movable submedian tooth, (c) 4 subequal, sharp intermediate denticles, (d) 1 slender intermediate tooth, (e) 1 sharp lateral denticle, and (f) 1 slender lateral tooth.

Basal segment of uropod with inner and outer carina, inner extending to dorsal spine; proximal segment of outer branch shorter than distal, with 5 slender, movable spines on distal margin, last long but not extending to end of distal segment; inner distal margin of proximal segment with rounded lobe armed with 7 stiff setae; inner branch of uropod triangular, with proximal portion of outer edge folded over; spines of basal prolongation flattened, trefoil, inner the longer.

Colour.—Pigment pattern largely faded in the only specimen examined; body with traces of scattered small, dark chromatophores; telson with distal median black patch, divided into two submedian halves by a clear area.

Measurements.—Male, TL 42.7; other measurements, in mm: carapace length, 7.7; cornea width, 1.3; rostral plate length, width, 2.0, 2.5; fifth abdominal somite width, 8.3; telson length, width, 3.5; 6.7.

Discussion.—The quadrangular rostral plate and spined median prominence on the telson of *H. osculans* will immediately distinguish it from *H. vercoi* (Hale) which it closely resembles; other differences have been pointed out under the discussion of

H. vercoi. The flattened telson with a single dorsal spine will distinguish *H. osculans* from *Heterosquilla brazieri* (Miers), and *H. tricarinata* (Claus), the only other species of the genus that occur in the same geographic area.

Distribution.—Known only from the southern coasts of Australia, where it has been recorded from Victoria, South Australia, and Western Australia. Bathymetric range not recorded.

Heterosquilla (Austrosquilla) vercoi (Hale, 1924)

Fig. 10

Lysiosquilla vercoi Hale, 1924, p. 499, pl. xxxiii, fig. 2, text-fig. 383.—Hale, 1927, p. 33, text-fig. 34.—Stephenson, 1953, p. 46; 1955, p. 3.—Stephenson and McNeill, 1955, p. 247.

Heterosquilla vercoi: Manning, 1963, p. 321 [listed; discussion].

Material.—1 ♀, 51.2; Kingscliff, S. of Tweed Heads, New South Wales; dug from sand on ocean beach, L.T.L.; 1953; Mrs J. Kirchner, col.; AM Reg. No. P. 12371.

Description.—Eye small, cornea subglobular, set obliquely on stalk and overhanging it laterally; outer margin of stalk with prominent, rounded projection; eyes extending slightly beyond end of second segment of antennular peduncle; eyescales small, erect, completely fused along midline.

Antennular peduncle short, about half as long as carapace; dorsal processes of antennular somite visible lateral to rostral plate as sharp, slender, anteriorly-directed spines.

Antennal scale small, less than half as long as carapace; antennal peduncle with 1 ventral papilla.

Rostral plate triangular, slightly broader than long, lateral margins convergent, concave on both sides of acute apex.

Carapace smooth, short, narrowed anteriorly, without carinae or spines.

Dactylus of raptorial claw with 19 teeth (reported range: 10-21), penultimate not markedly shorter than antepenultimate; outer margin of dactylus flattened, margin not strongly sinuate, with obscure angular projection at base; propodus slender, fully pectinate, with 5 movable spines at base of inner margin, proximal longest, next smallest; dorsal keel of propodus ending in blunt tooth; merus and ischium subequal in length; ischium slender, with prominent, sharp, subdistal tooth on lower margin.

Propodi of third and fourth thoracic appendages beaded ventrally, as broad as or broader than long, propodus of fourth broader than third and twice as broad as that of fifth appendage; propodus of fifth appendage as broad as long, with ventral brush of setae.

Mandibular palp absent; 5 epipods present.

Fifth thoracic somite lacking prominent lateral process and ventral spines; lateral processes of next 2 somites truncate, anterolateral angles more rounded than posterolateral; basal segment of first 2 walking legs with sharp inner and outer spines on posterior margin, last leg with outer spine only; inner branches of walking legs two-segmented, slender, that of last leg most elongate, that of first most ovate; eighth thoracic somite with low median keel on posterior margin of ventral surface.

Fig. 10.—*Heterosquilla* (*Austrosquilla*) *vercoi* (Hale), female, TL 51.2 mm, Kingscliff. *a*, anterior portion of body; *b*, submedian teeth and denticles of telson, ventral view; *c*, lateral processes of fifth, sixth, and seventh thoracic somites; *d*, basal prolongation of right uropod, ventral view; *e*, sixth abdominal somite, telson, and right uropod.

Abdomen smooth, depressed, without dorsal carinae; spines present at posterolateral angles of sixth somite only; anterolateral plates fully articulated; sixth somite with slender ventral spine in front of articulation of each uropod.

Telson noticeably broader than long, flattened, low median prominence terminating posteriorly in acute, blunt projection; marginal armature consisting of, on either side of midline, (a) 6 submedian denticles, inner smallest, (b) a movable submedian tooth, (c) 4 intermediate denticles, first and third shorter, stubbier than second and fourth, (d) a blunt intermediate tooth, (e) a lateral denticle, and (f) a slender, curved lateral tooth.

Basal segment of uropod with sharp inner and outer carinae, inner extending to slender dorsal spine; proximal segment of outer branch shorter than distal, with 6 slender distal spines, articulated at distal rather than outer margin, last extending well beyond midpoint of distal segment; inner distal margin of proximal segment with 11 setae on rounded lobe; inner branch elongate, curved, proximal portion of outer edge folded over; basal prolongation with 2 flattened, trefoil spines, inner longer.

Colour.—Rostral plate with 1, carapace with 2, and each body segment with 1 broad, diffuse band of brown chromatophores; eye-stalks mottled brown; antennal peduncles with anterior dark line; telson with black median distal spot, pigment interrupted along midline, and 2 diffuse lateral circles of dark pigment; each segment of uropod with scattered dark chromatophores.

Measurements.—Female, TL 51.2 mm; other measurements, in mm· carapace length, 8.1; cornea width, 1.5; rostral plate length, width, 2.3, 2.8; fifth abdominal somite width, 9.1; telson length, width, 4.8, 7.5.

Discussion.—*H. vercoi* is very similar to *H. osculans* but differs from that species as follows: (1) the rostral plate is triangular, not quadrangular; (2) there is but one papilla on the antennal protopod, not three; (3) there is an epipod on the fifth maxilliped; (4) the median prominence on the telson is blunt, not produced into a spine; (5) the intermediate denticles of the telson are small and only the second and fourth are slender; in *H. osculans* all four intermediate denticles are slender, and sharp.

The presence of only one dorsal projection on the telson will distinguish both *H. vercoi* and *H. osculans* from *H. tricarinata* and *H. brazieri.*

H. vercoi and *H. osculans* are the only two species in the genus in which the ischium of the raptorial claw is armed with an inferodistal spine.

Remarks.—The number of spines on the dactylus of the raptorial claw seems to be more variable than is usual in this species; from 10 to 21 teeth have been reported. The present specimen, which has 19, agrees in all other respects with Hale's original description; Hale's specimen had 11-12 teeth on the claw.

Distribution.—Known only from Australian waters, where it has been recorded from several localities between Southport, southern Queensland, and Robe, South Australia, and from Coles Bay, Tasmania. Shallow water.

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Sydney: V. C. N. Blight, Government Printer—1966

AUSTRALIAN BRACKISH WATER SERPULIDS (ANNELIDA: POLYCHAETA)

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Figures 1-3 Manuscript received 3rd February, 1965

SYNOPSIS

Evidence is presented to show that in the estuaries between Sydney and Brisbane there is a gradation from typical *Mercierella* to typical *Neopomatus* forms. On this evidence it is suggested that *Neopomatus* is synonymous with *Mercierella*, and *M. enigmatica* becomes the only brackish water serpulid known from Australia.

INTRODUCTION

Dew (1959) recorded only one species of brackish water serpulid (*M. enigmatica* Fauvel, 1922) from Australia, ranging from Townsville, Queensland, round the south of the continent to Carnarvon, Western Australia (fig. 1). She also states, "This species was first noted in Cooks River, Botany Bay, during 1910, when it was observed to have formed dense coral-like masses". Watson, McNeill, Johnson and Iredale (1936) commented on the presence of serpulids in the upper brackish reaches of the Brisbane River in 1929, but this material was neither identified nor preserved. Monro (1938) recorded *M. enigmatica* from the Swan River, Western Australia.

In Australia, *Mercierella* forms isolated populations in the brackish water regions of creeks and rivers. However, the species may be excluded from these areas by lack of a suitable substrate. A suitable substrate is one that provides a firm surface. Rocks, shells, vegetation, concrete, wood and glass are suitable while mud and sand are unsuitable. As many of the coastal creeks and rivers are very muddy, and lack rocks in their brackish areas, it is not surprising that distributional data gives a sparse and scattered picture.

Localities recorded by Dew (1959) are shown in fig. 1, though all her material has not been examined by the present author. The Australian Museum registered numbers and localities of Dew's material that has been examined are listed. Representative specimens from the author's collection have been placed in the Australian Museum, Sydney. The Australian Museum registered number is listed for each of these.

The material is listed commencing with the most northern locality, Ross River, Queensland, working south around the continent to Carnarvon, Western Australia. Material collected by others is acknowledged in the text. Where no acknowledgement is made, the material was collected by the author. The following abbreviations are used: R—river; Ck—creek; LWS—low water spring tide.

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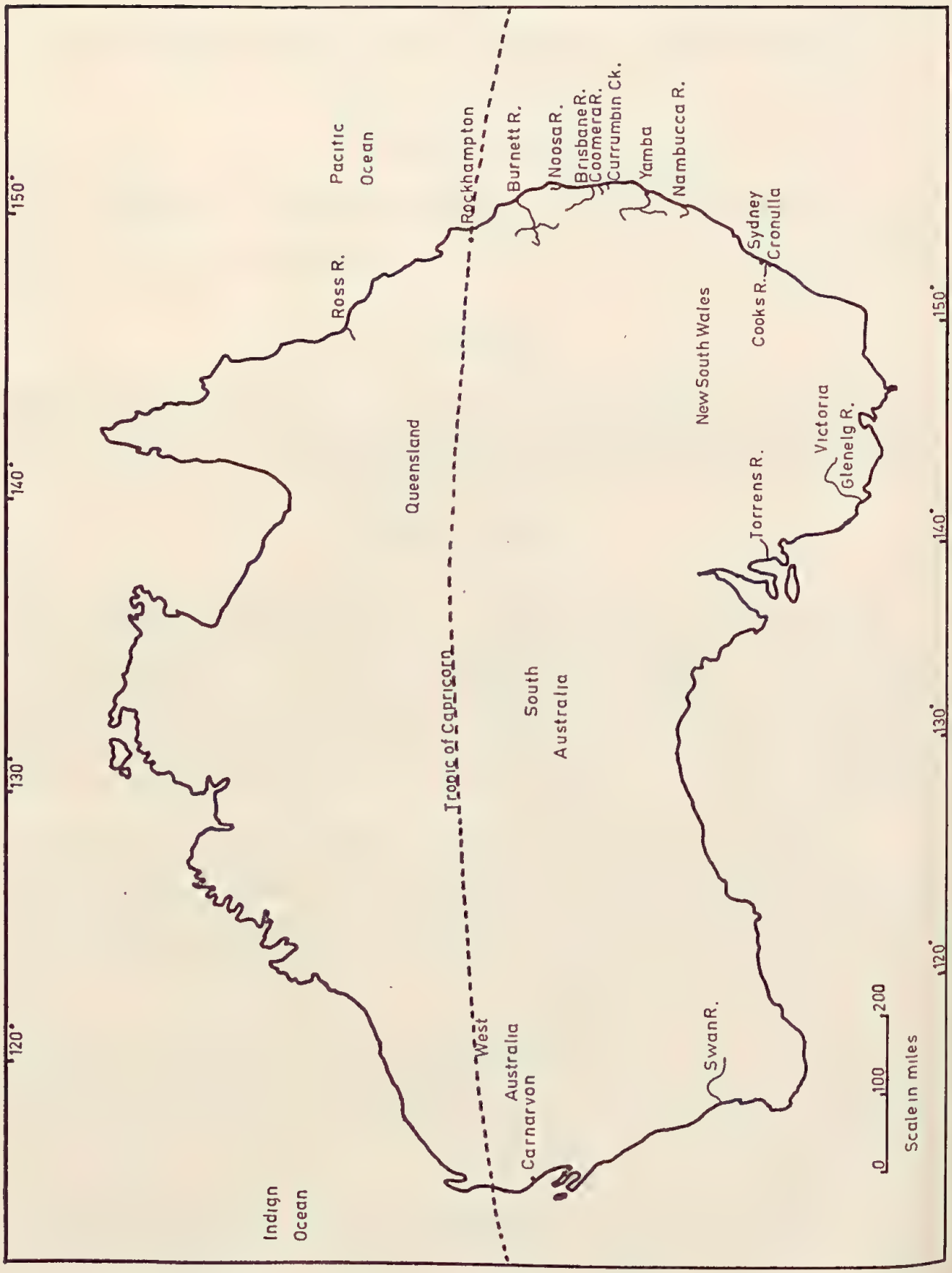

Fig. 1: Map of Australia, showing localities mentioned in text.

Genus **Mercierella** Fauvel, 1922

Type species: *Mercierella enigmatica* Fauvel, 1922.

Mercierella Fauvel, 1922, p. 424-30.

Neopomatus Pillai, 1960, p. 27-28.

Diagnostic features:

1. Operculum vesicular, armed with chitinous hooks, stalk smooth.
2. Collar setae of two kinds (1) simple, (2) deeply serrated; thoracic setae capillary; abdominal setae geniculate.
3. Uncini with few teeth, the last one being stouter and gouged.

Pillai (1960), working in Ceylon, described a new brackish water genus of serpulid, *Neopomatus*, containing two new species, *N. uschakovi* and *N. similis*, the latter also containing a variety, *rugosus*. Table 1, taken from Pillai (1960), gives the main characters of both genera as defined by Pillai. Specimens of brackish water serpulids collected in Queensland fit the description of this genus, while those collected from Sydney south around the continent to Carnarvon are referable to *Mercierella*.

1. *Operculum.* Pillai (Table 1) does not successfully differentiate between the form of the operculum in the two genera as it is possible for a vesicular operculum to be non-calcareous and vice versa. Fauvel (1922) stated that *Mercierella* has a vesicular operculum; Queensland specimens have such operculae while, in those from Sydney, the upper part becomes white and leathery with age. In material collected from the Nambucca River, approximately half-way between Brisbane and Sydney, the operculum is vesicular on living material but often becomes white and leathery externally after alcohol preservation. Dew (1959, p. 31) described the operculum as being "non-calcareous, cone shaped; somewhat vesicular, top slightly depressed". In the Queensland and Nambucca River specimens the top is either flat or slightly convex. Fauvel (1923) states that it is slightly concave on top.

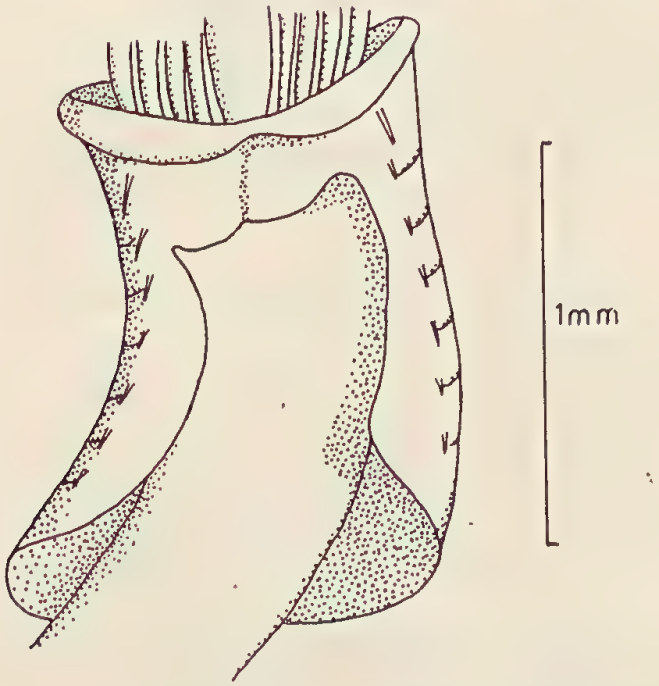

Fig. 2: Dorsal view of the thoracic region of *M. enigmatica* specimen from the Nambucca River with the thoracic membrane joined for the anterior third only.

The typical *Mercierella* operculum bears movable, inwardly directed hooks, while that of *Neopomatus* bears outwardly directed spines which are projections from the surface of the operculum and are not movable. Both types of projections are arranged in concentric rings. Rioja (1924, 1943) figures the typical *Mercierella* hooks, describing them in detail, and in describing specimens from the Argentina coast (1943) he says that in the interior of the opercular crown some of the spines are "soldered" and continuous with the opercular plate. It appears from this that Rioja had some specimens bearing both hooks and spines.

2. *Collar and thoracic membrane.* Pillai (pers. com.) regards the dorsal joining of the lateral lobes of the collar and thoracic membrane (Pillai, 1960, fig. 12a) as being the most important character separating *Neopomatus* from all other genera and has "not come across one specimen with a free thoracic membrane". Sydney specimens have a free thoracic membrane and collar, while both are joined dorsally in Queensland specimens. This character is variable among specimens collected from the Nambucca River. In some, collar and thoracic membrane are completely joined dorsally, while in others they are partially joined dorsally and varying lengths of the posterior thoracic membrane are free (fig. 2). In yet others there is no dorsal joining. This variation seems independent of specimen size (table 2).

Fig. 3: Collar setae from specimens from different localities—(1) Cooks River, (b) and (c) Nambucca River, (d) and (e) Brisbane River.

3. *Collar setae.* The types of collar setae serration recorded at the Cooks River (Sydney), Nambucca River, and Brisbane River are shown in table 3 with the different basal modifications illustrated in fig. 3. Fig. 3a, b, e illustrate setae with the number of basal teeth increased, fig. 3c shows setae with a smooth portion of

the shaft near the base, while fig. 3d shows collar setae with a single row of teeth. Modifications of the basal (= Pillai proximal) serrations have been recorded at all three stations. A few specimens from Sydney had two rows of serrations on the collar setae basally, with a reduction to one row towards the tip.

Fauvel (1922) stated there are two rows of sharp teeth on the collar setae, while in 1932, p. 249, "strongly serrated setae with two longitudinal rows of teeth, a few transverse rows at the base and without an intervening smooth part of the shaft." Dew (1959) also records two rows of teeth.

Rioja (1924) describes *Mercierella* specimens with large teeth and smaller ones laterally. He also states that the lower part of the shaft may have two or three rows of bristles which become reduced to one row in the upper part. Fauvel (1927, fig. 123g, h) figures collar setae with three lateral teeth at the base. The proximal teeth in *N. uschakovi* are modified in that they have a jagged or serrated edge and one large tooth is thus modified to form three (Pillai, 1960). Hence collar setae serration is variable in both *Mercierella* and *Neopomatus* with an overlap between both groups.
4. *Uncini.* Both genera have a similar number of uncinal teeth, *Neopomatus* with six and *Mercierella* with five to nine. The uncini of both have a basal bifid process, not as well defined in *Mercierella* but illustrated by Fauvel, 1922. Both have the lowest tooth gouged, although in *Neopomatus* not to the same extent as in *Mercierella.* Therefore both types of uncini are basically similar.

5. *Tubes.* Coloration is the main difference, but *Mercierella* tubes often become an "orange brown" as they are exposed to fresh water. Specimens from Queensland and the Nambucca River have a wide variety of forms in a sparse population—round or rectangular, with or without one-three longitudinal ridges, with or without peristomes—but in dense populations they are round with peristomes.

The characters of the operculum, thoracic membrane, and collar setae of *Mercierella* as described by Dew (1959) from Sydney, and of specimens from Cooks River, Nambucca River, and Brisbane River are compared in table 4. The type of uncini and tubes are basically the same in both groups, with a greater variety of the former in *Mercierella* and of the latter in *Neopomatus.*

Therefore there is a continuous south to north cline between Sydney and Brisbane in the characters used to separate *Mercierella* from *Neopomatus.* This cline is continuous between isolated populations, suggesting that it may be temperature controlled. It is possible that a similar cline occurs in the northern hemisphere, because while *Mercierella* is recorded from Ennur Bachwater, India (Fauvel, 1932), *Neopomatus* occurs in Ceylon (Pillai, 1960). *Neopomatus* material has also been collected from British North Borneo.

Mercierella enigmatica Fauvel, 1922

Mercierella enigmatica Fauvel, 1922, p. 424, fig. 1; Monro, 1924, p. 155, fig. A-E; Rioja, 1924, p. 160, fig. 1-30, pl. 5, fig. 1-3; Fauvel, 1927, p. 360, fig. 123; Fauvel, 1931, p. 1067; Fauvel, 1932, p. 249; Fauvel, 1933, p. 185; Monro, 1938, p. 624; Mensil and Fauvel, 1939, p. 37; Rioja, 1943, p. 547, 2 figs; Dew, 1959, p. 31, fig. 22.

Neopomatus uschakovi Pillai, 1960, p. 28, figs. 11, 12.

N. similis Pillai, 1960, p. 32, fig. 12.

N. similis rugosus Pillai, 1960, p. 33.

Diagnostic features: As for genus.

Material examined. Numbers prefixed by "W." refer to registered numbers in the Australian Museum.

AUSTRALIA

Queensland: Ross R., Townsville, W.4144, railway bridge pylons, zone 2 feet 6 inches wide extending up from L.W.S., abundant, Aug. 4, 1964; Ross R., W.4133, rocks on downriver side of first weir, zone 6 inches wide below L.W.S., common, Aug. 4, 1964; Townsville, W.3778, c. 6 specimens. B. Dew, Mar. 1, 1951; Townsville, W.3781, B. Dew, 1950; Rockhampton, rocks at the Causeway, tubes containing dead animals, zone 1 foot wide extending up from L.W.S., common, Nov. 29, 1963; Burnett R., W.4136, rocks on river bank near wharf, zone 2 feet 6 inches wide extending up from L.W.S., abundant, Oct. 2, 1963; Noosa R., W.4135, rocks 2 miles upriver zone 6 inches wide below L.W.S. common Jan. 17, 1961, Dec. 14, 1962; Noosa R., rocks in L. Cooroibar, zone 6 inches wide below L.W.S., present, Jan. 16, 1961; Noosa R., rocks in L. Cootharaba, zone 6 inches wide below L.W.S., present, Jan. 16, 1961; Noosa, W.3777, c. 8 specimens, B. Dew, Dec. 26, 1950; Pine R., rocks at mouth, L.W.S., present, Oct. 1960; Pine R., 4 miles upriver, rocks in shallows below L.W.S., common, Oct., 1960; Pine R., Petrie, rocks in shallows from L.W.S. down 1 foot, common, Oct., 1960, Dec., 1961; Brisbane R., 8 miles upriver, wharf piles and rocks, from 2 feet above to 2 feet below L.W.S., varying common to abundant between Feb., 1960 and Oct., 1964; Brisbane R., W.4141, 14 miles upriver, wharf piles and rocks, from 3 feet above to 5 feet below L.W.S., varying common to abundant between Feb., 1960 and Oct., 1964; Brisbane R., 20 miles upriver, rocks, zone 3 feet wide around L.W.S., varying common to very common between Feb., 1960 and Oct., 1964; Brisbane R., 28 miles upriver, rocks, zone 6 inches wide around L.W.S., present between Feb., 1960 and Oct., 1964; Coomera R., rocks below weir, zone 6 inches wide below L.W.S., common, Oct., 1960, absent, May, 1961; Nerang R., W.4140, Southport, rocks, zone 6 inches wide below L.W.S., present, June, 1960; Tallebudgera Ck, 2 miles upstream, rocks, zone 6 inches wide below L.W.S., common, July, 1960; Currumbin Ck, 3 miles upstream, rocks in shallows, zone 6 inches wide below L.W.S., common, July, 1960.

New South Wales: Yamba, W.3779, 2 specimens, B. Dew, Sept. 1, 1950; Nambucca R., W.4137, Macksville, rocks, zone 1 foot wide below L.W.S., common, Aug., 1962, very common, Jan., 1964; Cooks R., W.4139, Tempe, Reef structure visible at L.W.S., abundant, Wisely, 1960, Jan., 1964; Cronulla, Shell Pt., W.3775, 15 specimens, B. Dew, July 1, 1950.

Western Australia: Swan R., W.4134, Crawley, fouling plates, very common; J. Lucas, Feb., 1964; Swan R., Chidly Pt., W.3776, 4 specimens, B. Dew, Mar. 9, 1951; Perth, W.3780, 1 specimen, B. Dew; Carnarvon, W.3774, 100 specimens, G. Chittleborough, Oct. 8, 1951.

BRUNEI

Submerged *Agnathis alba* planks, common, Hancock and Gore, 1962.

CEYLON

Negombo Lagoon, W.4138, 50 specimens, T. G. Pillai, Apr. 10, 1964.

U.S.A.

Aquatic Park Lane, Berkeley, California, abundant, Ralph I. Smith, Jan., 1961, J. Nelson, 1964.

CONCLUSION

As there is a continuous cline between isolated populations between Sydney, where the brackish water serpulids are typical of *Mercierella*, and Brisbane, where the brackish water serpulids are typical of *Neopomatus*, *Neopomatus* Pillai, 1960, has been synonymized with *Mercierella* Fauvel, 1922. *Neopomatus uschakovi* Pillai, 1960 and *Neopomatus similis* Pillai, 1960, have both been synonymized with *Mercierella enigmatica* Fauvel, 1922.

ACKNOWLEDGEMENTS

This work was carried out while I was a Commonwealth Post-graduate (Ph.D.) student, and is part of a project financed jointly by this scholarship and the University of Queensland. The work was supervised jointly by Professor W. Stephenson and Dr R. Endean, both of whom I wish to thank for their comments and helpful criticism.

My thanks are due to those who have collected material and to the Director of the Australian Museum and Miss Elizabeth Pope, for making available material housed at the Australian Museum. I also wish to thank Miss Barbara Dew for making available material which previously had only been stored at the Australian Museum.

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TABLE 1

	Neopomatus	*Mercierella*
1.	Operculum vesicular, with or without one or more rows of small outwardly directed denticulations.	Operculum non-calcareous, crowned with concentric rows of somewhat long, inwardly directed spines.
2.	Collar and thoracic membrane of the two sides are fused to form a continuous membrane between the setigerous fascicles of the two sides over the dorsal thoracic wall.	Collar and thoracic membrane of the two sides with free dorsal edges.
3.	Collar setae with a single row of stout teeth, a few of the proximal ones being usually modified.	Collar setae with two rows of sharp teeth.
4.	Uncini with relatively few teeth and a basal bifid process.	Uncini with the lowest tooth gouged.
5.	Tubes white or coloured orange or red, with or without remnants of successive peristomes. Found in more or less dense groups or masses. One or three ridges may be present.	Tubes white, circular in cross-section, with collar-like remnants of successive peristomes, and growing in masses.

Table 1—Part of table 1 (Pillai, 1960) comparing the main diagnostic features of *Neopomatus* and *Mercierella*.

TABLE 2

Length of animal	*Length of thorax*	*State of thoracic membrane*
3.5	1.0	Joined throughout dorsally.
6.0	1.5	Both sides free dorsally.
5.0	1.2	Both sides joined for anterior $\frac{1}{3}$ dorsally.
5.0	1.3	Both sides joined for anterior $\frac{2}{3}$ dorsally.
6.0	1.5	Both sides joined for anterior $\frac{1}{2}$ dorsally.
5.0	1.3	Both sides free dorsally.
4.0	0.8	Both sides joined for anterior $\frac{3}{4}$ dorsally.

Table 2—A comparison of the total length and length of the thorax with the state of the thoracic membrane on *M. enigmatica* collected from the Nambucca River (N.S.W.). All measurements are given in mm.

TABLE 3

Locality	*2 rows of teeth*	*Basally 2-3 teeth 1 row above*	*Smooth shaft between basal and upper teeth. 1 row teeth*	*1 row teeth*
Sydney	+	+		
Nambucca R.		+	+	+
Brisbane R.		+		+

Table 3—A comparison of the type of collar setae found at three Australian localities.

TABLE 4

Locality	*Operculum*	*Thoracic membrane*	*Collar setae*
Sydney (B. Dew)	M	M	M
Cooks R.	M	M	MN
Nambucca R.	N	MN	N
Brisbane R.	N	N	N

Table 4—A comparison of *Mercierella* and *Neopomatus* characters (as defined by Pillai, 1960) of specimens collected from Sydney north to Brisbane. M and N indicate that the characters are as described for *Mercierella* and *Neopomatus* respectively. On two occasions (MN) characters of both types are present.

Sydney: V. C. N. Blight, Government Printer—1966

SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part I: Anatomical Features

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Plates 16–23. Figs 1–7.

Manuscript received, 30th March, 1965

This study of the anatomical and metrical features of the skull and teeth of bandicoots of the genus *Perameles* was undertaken in order to analyse age, sex, and locality variations and trends. It is hoped that the results of the study will assist in the assessment of intra- and inter-specific taxonomic, phylogenetic and ecological relationships, enable the various subgeneric taxa to be more clearly defined, and facilitate the identification of subfossil and fossil fragments and isolated teeth.

The present section of the study, Part I, outlines the taxonomy of the genus *Perameles* and describes generally the material used in the whole study. It also includes an illustrated, anatomical description of the skull and teeth of *Perameles nasuta* and a discussion of the anatomical variations of these features in other members of the genus *Perameles*.

TAXONOMY

With regard to the taxonomy of the long-nosed bandicoots, most of the early studies, such as that by Waterhouse (1846), included rather superficial accounts of a number of not very clearly defined species. However, in 1888 Thomas gave comprehensive descriptions and reliable keys to most of the species still currently recognised. In this study, Thomas recognised three genera (*Perameles*, *Peragale*, and *Chaeropus*) in the family Peramelidae. In the most recent studies, Simpson (1945) divides this family into five genera: *Perameles* (which includes *Peroryctes*), *Echymipera*, *Thylacomys* (syn. *Macrotis*, *Paragalia*), *Chaeropus*, and *Thylacis* (= *Isoödon*); whilst Tate (1948) describes eight genera of bandicoots: *Perameles*, *Isoödon*, *Macrotis*, *Echymipera*, *Peroryctes*, *Chaeropus*, *Rhynchomeles*, and *Microperoryctes*. The genus *Perameles* in the present study is taken to include the long-nosed bandicoots of Australia only, i.e., the genus as defined by Tate.

At the specific level, Iredale and Troughton (1934) classified the long-nosed bandicoots as follows:

Genus: **Perameles** Geoffroy, 1803

Long-nosed bandicoot

Perameles nasuta nasuta Geoffroy, 1804. N.S.W., Victoria, South Queensland.

Perameles nasuta pallescens Thomas, 1923. North Queensland.

G 23272—1

Fig. 1.—Map of Australia, including State boundaries, to show the distribution of *Perameles* material examined. Circles, *P. nasuta;* squares, *P. gunnii;* triangles, *P. bougainville* group; blacked-out, one specimen; numbered, number of specimens; ?, locality uncertain.

Orange-backed bandicoot

Perameles eremiana Spencer, 1897. Central Australia.

Eastern barred bandicoot

Perameles fasciata Gray, 1841. N.S.W., Victoria.

Tasmanian barred bandicoot

Perameles gunnii Gray, 1838. Tasmania.

Marl, or western barred bandicoot

Perameles myosura myosura Wagner, 1841. South-western Australia.

Perameles myosura notina Thomas, 1922. South Australia.

Little marl

Perameles bougainville Quoy and Gaimard, 1824. Mid western Australia and Islands of Shark Bay.

In a more recent taxonomic review of the genus *Perameles*, Tate (1948) made the following comments: He expressed doubts as to whether the differences between the northern and southern *P. nasuta* specimens should be maintained and he felt that *P. myosura* was "at best a race of *bougainvillei*". His final suggestions were that "the small bandicoots *P. bougainvillei*, *fasciata*, *notina*, and *eremiana* may be local races of a single widespread southern species, or, if this is not so, that they may be members of a single species-group, as opposed to the larger northeastern *Perameles nasuta*. To this species-group I would add the much larger *gunnii* as a full species".

Discussing *Perameles* in 1962, Marlow retained the two subspecies of *P. nasuta*, the full species *P. gunni*, *eremiana*, *fasciata*, and *bougainvillei*, but dropped *P. myosura myosura* and made *P. myosura notina* a subspecies of *P. bougainvillei* (*P. b. notina*). His distributions for the various species follow those of Iredale and Troughton (1934) fairly closely, although, in general, his distributions are rather more restricted. However, the range of *P. gunni* is extended to include the southern part of Victoria.

From the foregoing taxonomic resumé, it would appear that the species *P. nasuta* and *P. gunnii* are clearly valid, whilst there is some doubt about the status of the smaller species of *Perameles* which have been described under the names *fasciata*, *eremiana*, *myosura*, and *bougainville*. Consequently, for the purpose of the present study, it was decided initially to consider the available material in three groups, (a) *P. nasuta*, (b) *P. gunnii*, and (c) *P. bougainville*—the latter to include the four smaller species. The present paper will consider anatomical features and variations of the skull and teeth within and between these three groups; succeeding papers will deal with metrical aspects.

(*Note:* There has been confusion in the published literature about the correct spelling of the names of *P. gunnii* and *P. bougainville*, as can be seen from the above outline of past taxonomy, where the spelling used by the respective authors has been retained. The spelling, as given by the original authors, is *P. gunnii* (Gray, 1838) and *P. bougainville* (Quoy and Gaimard, 1824). The name *P. bougainville* has been tentatively used for group (c) as it was the first described species of the group and thus has priority.)

MATERIAL

The *Perameles* material described in this study was loaned to me by the following Institutions: The Queensland Museum, Brisbane; The Australian Museum, Sydney; The Macleay Museum, Sydney; The National Museum of Victoria, Melbourne; The Fisheries and Wildlife Department, Melbourne; The Queen Victoria Museum and Art Gallery, Launceston; The Tasmanian Museum and Art Gallery, Hobart; The South Australian Museum, Adelaide; and The Western Australia Museum, Perth. My sincere thanks are due to the Directors and relevant Staff Members for their courtesy and co-operation.

In addition to the above material, Dr A. G. Lyne, C.S.I.R.O., Prospect, N.S.W., lent me some particularly useful *P. gunnii* specimens, and twenty-one *P. nasuta* specimens from Sydney, N.S.W., were specially collected and prepared for this study by Mr A. B. Bailey, Department of Anatomy, University of Sydney, Sydney, N.S.W.

The total number of skulls examined was 205: (a) *P. nasuta*—111; (b) *P. gunnii*—51; and (c) *P. bougainville* group—43. The distribution of this material is shown in Fig. 1. Of *P. nasuta*, the Queensland specimens (20 males and 9 females) are sparsely scattered, mainly along the coastal strip, from Cooktown in the north to Tambourine in the south; the New South Wales specimens (19 males and 35 females), except for one specimen which comes from further afield, were all collected within a radius of 50 miles of Sydney; the Victorian specimens (15 males and 13 females) are, bar one from the south-west, all from the south-eastern half of that State. Of *P. gunnii*, 14 males and 9 females come from the south-western corner of Victoria, with possibly some slight overlap into south-eastern South Australia; 12 males and 16 females come from various localities in Tasmania. The *P. bougainville* group can initially be considered in 3 subsections (Fig. 1): (i) south-western South Australia (12 plus 1) and south-eastern Western Australia (3 plus 1); (ii) 5 specimens from Dorre and Bernier Islands in Shark Bay off the central west coast of Western Australia; and (iii) 5 specimens scattered through the western part of central Australia, i.e., eastern Western Australia (2 plus 1), south-western Northern Territory (1) and north-western South Australia (1). The 16 (?) specimens included in Fig. 1, as will be discussed later, fit on size and anatomy in subsection (i). No specimens from south-western Western Australia (*P. myosura myosura*) or from western New South Wales and Victoria (*P. fasciata*) were found in the available material in Australia. Certain specimens labelled *P. fasciata* (National Museum of Victoria) are clearly *P. gunnii*. The sex distribution of the *P. bougainville* material has not been included above, as few specimens are of known sex and, as will be shown later, sexual dimorphism is not clearly apparent in the skulls and teeth of these specimens.

The material used in this study has been collected over a considerable period of time, some dating into the latter part of the last century, and some being collected in the past year. Because of this, the distribution of the genus, as shown in Fig. 1, may not necessarily represent the present distribution, as the ranges have been steadily shrinking over the years with the fuller utilisation of the land for settlement and agriculture. (Similarly, it should be noted that many areas have clearly not been sampled and absence does certainly not imply that the genus is not present.) Temporal differences may occur in the material, but the sample was inadequate for any tests of the possibility.

As will be discussed below, the sexing of *P. nasuta* skulls by the anatomy and size of the canine teeth is fairly simple and it is similarly possible, although sometimes more difficult, to sex *P. gunnii* skulls by this method. In the *P. bougainville* group sex dimorphism in the non-metrical features is not apparent.

With regard to the age of the individual specimens, a skull was considered to have come from an adult when all of the teeth were fully erupted and in use. However, it is clear that some skull growth occurs subsequent to this stage. On the basis of a very small sample (partial records from 6 specimens) it appears from Lyne (1964) that the rate of growth in head length in *P. nasuta* is very rapid up to 100 days, slows quite markedly between 100 and 200 days and then drops to a very slow rate which, however, continues at least until about 375 days, when the records cease. On even more limited material, it appears from Kingsmill (1962) that the last tooth (P3) emerges some time between 137 and 361 days. From this admittedly very inadequate data (and for practical necessity) it would appear that the full emergence of P3 (and the canine, particularly in the male) are the most suitable available criteria for calling a specimen adult, despite the fact that some slight further growth of the skull undoubtedly occurs.

THE ANATOMY OF THE SKULL AND TEETH OF P. NASUTA

The main features of the cranium and mandible of *P. nasuta* are described by a series of notes dealing with points of particular taxonomic value, by four labelled drawings, (figs 2–5) and by three photographs (plates 16, 21, and 22). (In addition, a number of photographs of standard views of *P. nasuta* will be included in Part II of this study.) The anatomy of the cranium and mandible of the American marsupial, *Caenolestes*, which is very similar to that of *P. nasuta*, has been described in considerable detail by Osgood (1921). Reference should be made to that study for aspects of cranial anatomy not considered here, such as internal structure and the names of foramina.

With regard to the dentition of *P. nasuta*, a full, illustrated account of dental anatomy, eruption sequence, occlusion, and attrition is included. Terminology for the teeth basically follows that of Gregory (1922).

Sexual dimorphism (except in size) is not apparent in the cranium or mandible of *P. nasuta*, but in the teeth, the canines of the two sexes differ considerably in both size and anatomical details. Thus, except for the canine teeth, the descriptions which follow (for *P. nasuta* and for the other *Perameles* species) are applicable to both males and females.

(a) *Cranium:* The following features of the cranium are of particular interest (see figs 2–5, plate 16 and plates 21 and 22):

(1) The muzzle is very considerably elongated by the forward growth of the maxilla, premaxilla and nasal bones. The cartilagenous nasal septum extends forward about another 6 mm beyond the premaxillae and nasals. The prolongation of the premaxilla anterior to the incisors is an unusual feature and is probably correlated with the habit of burrowing small holes with the tip of the muzzle in the search for insects in the ground.

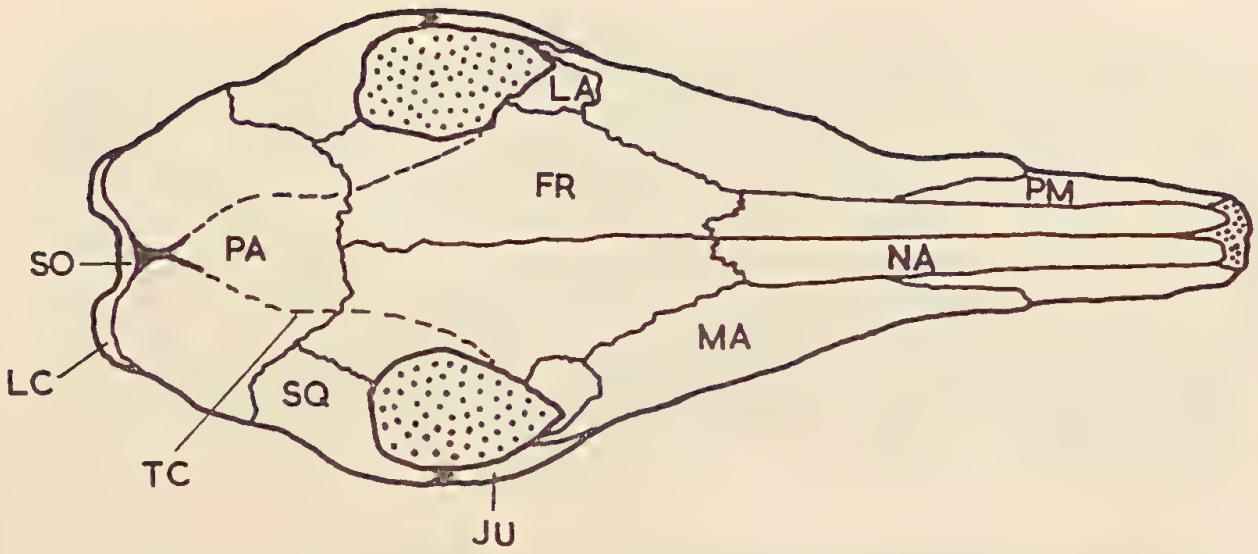

Fig. 2.—Drawing of dorsal view of *P. nasuta* cranium. Key to labelling Figures 2 to 5: AB alisphenoid bulla, APV anterior palatine vacuity, AS alisphenoid, BO basioccipital, BS basisphenoid, CO condyle, EO exoccipital, FM foramen magnum, FR frontal, JU jugal, LA lacrimal, LC lambdoid crest, MA maxilla, MS mastoid, NA nasal, PA parietal, PL palatine, PM premaxilla, PO periotic, PPV posterior palatine vacuity, PS presphenoid, PT pterygoid, SO supraoccipital, SQ squamosal, TC temporal crest (line), TY tympanic.

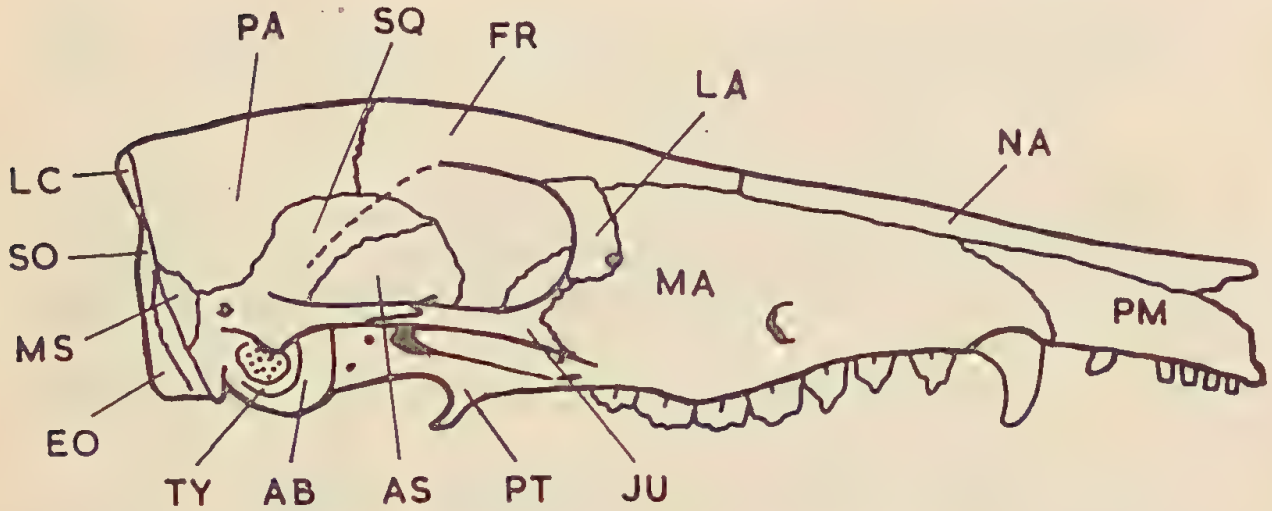

Fig. 3.—Drawing of lateral view of *P. nasuta* cranium (male)

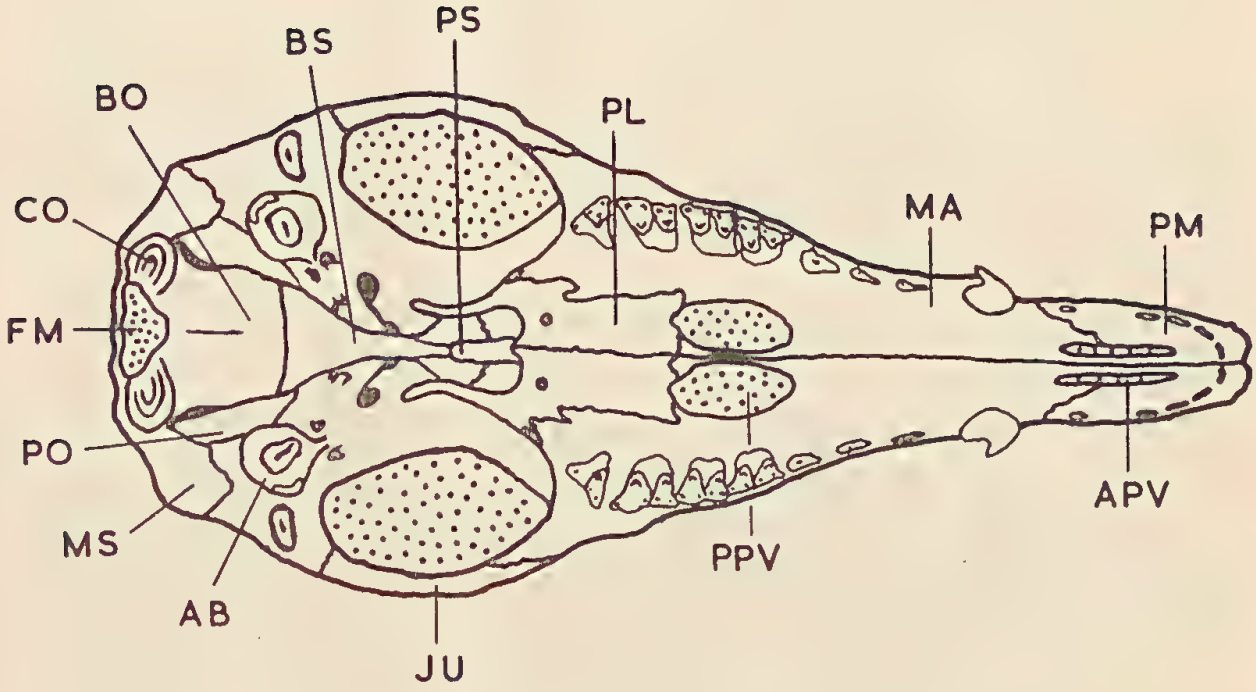

Fig. 4.—Drawing of ventral view of *P. nasuta* cranium (male)

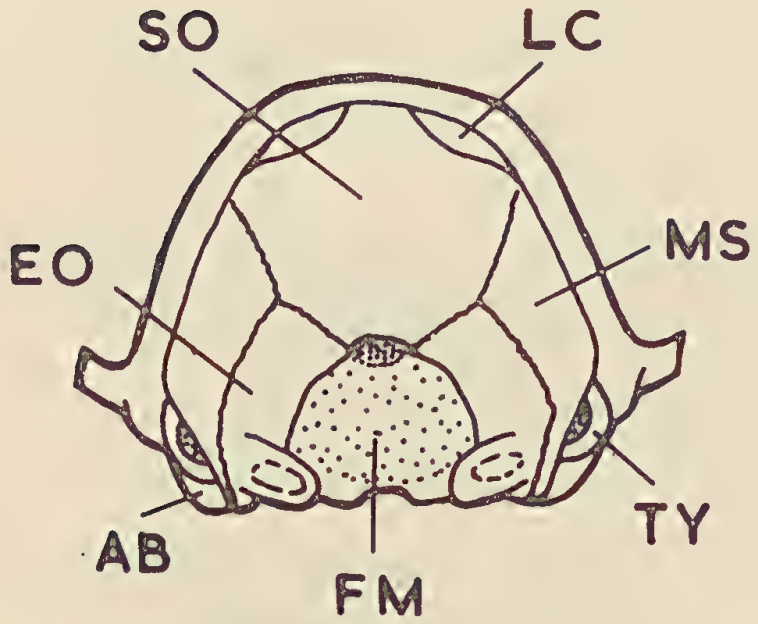

Fig. 5.—Drawing of posterior view of *P. nasuta* cranium

(2) The temporal lines on the dorsal surface of the calvaria are usually not very prominent. The lines of the two sides generally join posteriorly to form a short, weak sagittal crest.

(3) The occipital or lambdoid crests are well developed, particularly superiorly where they form large, posterolaterally-projecting protuberances on either side of the midline.

(4) The palate is very long and narrows markedly from the premolars forward. The paired anterior palatal vacuities are long and thin, whilst the posterior pair have usually lost their thin median partition and together form a single, very large opening. At the level of M^3 and M^4 the palate is very thin, but only occasionally (usually posterior to M^4) are there any other palatal vacuities and these are generally few, small, and asymmetrical.

(5) The alisphenoid bullae are not markedly inflated; the tympanic bone is crescent-shaped and is not fused onto the alisphenoid.

(6) The zygomatic arches are very slender and arched laterally.

(7) The foramen magnum is large and the two condyles lie on either side of the ventral margin. There is a large characteristic notch in the middle of the dorsal margin of the foramen magnum. The notch separates the two exoccipital bones and is situated in the position where Kerkring's centre of ossification may be found during the development of the human cranium.

(8) A considerable part of each lacrimal bone extends onto the dorsolateral surface of the muzzle adjacent to the orbit. The foramen for the lacrimal duct is found in this part of the lacrimal bone.

(9) The infraorbital foramen, which lies on the lateral side of the muzzle, just above M^1, is very large.

(10) The sutures of the cranial vault and base (including the sutures between the supra-, ex- and basi-occipitals and also the one between the basioccipital and the basisphenoid) usually remain patent, or at least are clearly visible, throughout the animal's life. An exception is the interparietal suture which is obliterated almost completely in all except one of the specimens examined. This suture closes, as a rule, at about the time the last teeth are erupting.

(11) With advancing age, the crania in both sexes become more rugged. This applies particularly to the amount of development of the temporal, sagittal, and lambdoid crests. There is also a strong suggestion that overall size continues to increase well after the last tooth has erupted and is in use.

(b) *Mandible* (plate 16):

(1) The coronoid process is very high and marked off from the condyle by a deep notch.

(2) The gonial angle is very obtuse; the angular process is well developed.

(3) The masseteric fossa is large and fairly deep.

(4) The two halves of the mandible do not synostose at the symphysis.

(c) *Dentition:*

(i) *Deciduous:* In *P. nasuta*, as in most marsupials, there is only a single deciduous tooth in each quadrant of the jaws. The tooth is generally designated as the last premolar, dp3 (Wilson and Hill, 1897). In both jaws the tooth is similar, relatively simple in structure and minute in size. In the unworn state, the mesial end of the tooth is considerably higher than the rest of the tooth and forms a prominent cusp; at the distal end, there is a suggestion of a much smaller, lower cusp. Unworn, the mesiodistal diameter is usually the greater, but, in a worn tooth, the buccolingual measurement may on occasions be larger. The occlusal surface of the crown of a worn tooth eventually forms a homogeneous concavity, circular or oval in outline. In both jaws dp3 is replaced by the last permanent premolar.

(ii) *Permanent:* The adult dental formula is: $\frac{5 \cdot 1 \cdot 3 \cdot 4 \cdot}{3 \cdot 1 \cdot 3 \cdot 4 \cdot}$ In occlusal view, the sides of the upper dental arcade lie close together anteriorly and are almost parallel up to the canines. The buccal surfaces of the two sides then broaden out in the region of the premolars and M^1 and finally converge very slightly at M^4 (plate 17). Because of the considerable inward projection of the large molars, this broadening out is not as marked when the lingual surfaces of the teeth are followed. The two sides of the lower dental arcade (plate 19) diverge evenly from anterior to posterior when the lingual surfaces are considered, but the broad molars bulge outwards when the buccal surfaces are viewed. From the side (plate 16), the occlusal surfaces of the upper teeth form a sinuous curve, concave downwards from the mesial incisor to the last premolar, and convex downwards from there to the distal end of the toothrow. The occlusal surfaces of the lower teeth form a weaker reciprocally curved profile (plate 16); but in both jaws, the line is interrupted (particularly in the male) by the large canine teeth. The three premolars in *Perameles* have been designated P_1, P_2, and P_3 (Wilson and Hill, 1897 and Bensley, 1903), but their homologies are considered uncertain. Sexual dimorphism is only found in the canines. The term "crown" has been used to denote that portion of the tooth which normally lies above the alveolar margin.

(1) *Upper teeth* (plates 16 and 17): The first four upper incisors of each side are small teeth, buccolingually (labiolingually) flattened and relatively long mesiodistally. I^1 is considerably smaller than I^2, I^3, and I^4, which are subequal. I^1 leans slightly lingually and the mesial part of I^2 may also lean inwards slightly. The left and right I^1 are separated by a small diastema, but the other adjacent teeth of this group either touch or almost touch. I^1–I^4 of the two sides form a parabolic arch on the premaxilla. I^5 is similar in size to I^2–I^4 in its mesiodistal and buccolingual dimensions, although in the former measurement, it is usually slightly shorter. In the height dimension, this tooth is considerably larger than any of the other incisors. In shape, I^5 is distinctly caniniform with a clearly pointed tip; viewed from the side, it is directed slightly backwards, i.e., posteriorly. I^5 is separated from both I^4 and the $\underline{C}$ by a diastema, each of which measures about 3.5 mm. Only the incisal half of the crown of each of the incisors is enamel-covered, i.e., only the incisal half of the tooth above the alveolus.

The $\underline{C}$ tooth has a large root which, particularly in the male, forms a prominent eminence on the external surface of the maxilla. Within its alveolus, starting from the apex, the root first runs anteriorly and then curves sharply ventrally just before it emerges from the alveolus. The tooth is almost invariably much smaller in the

female than in the male (see Part II) and, in addition, also differs anatomically (plate 18). The male C tooth is very large, particularly in mesiodistal length, as it leaves its alveolus. The crown portion is of considerable height and tapers evenly and gradually as it curves towards its tip. Only about the incisal 1/3 of the crown is enamel-covered. In the female, the crown of the C is not nearly as high as in the male. The sides of the basal half of the crown are parallel, but thereafter the crown tapers rapidly to a point, the mesial edge being convex and the distal edge concave. Only the incisal, tapered portion is enamel-covered in this sex and it is marked off from the basal part by very small mesial and distal cuspules. In both males and females the C is considerably flattened buccolingually. Although the C teeth are so different in the mesiodistal length in the two sexes, the diastemata separating these teeth from I^5 and P^1 respectively, are of similar length in the two sexes.

Of the upper premolars, P^2 is slightly larger than P^1, and P^3 is considerably larger than P^2 (plate 16). In shape, P^1 and P^2 are very similar. They are buccolingually flattened teeth with a large central cusp and very small mesial and distal cuspules. Seen from the occlusal surface (plate 17), P^3 is somewhat triangular in outline, with the buccal surface forming the base and the apex being situated slightly distal to the centre of the tooth, on the lingual side. On the buccal side of the tooth, there is a large central cusp, a very small mesial cuspule and a fairly prominent distal cuspule. In addition, there is a moderate sized cuspule on the lingual side, which may be separated from the large central cusp on the buccal side by a small furrow or fovea. Each premolar has a mesial and a distal root; the roots of P^3 (particularly the distal one) being the largest in cross-sectional area. The two roots of each being premolar, especially P^1 and P^2, join the crown well below (i.e., ventral to) the general level of the palate. Bony downgrowths from the alveolar margin of the maxilla project over the buccal and lingual sides of each of the premolars and cover their central portions (i.e., mainly the region where the roots join). In life, the basal portions of the premolars (and also of the molars) are covered by the very thick, tough, mucous membrane which lines the mouth.

The diastemata between the teeth were not measured for the metrical study of *P. nasuta* (Part II), but some measurements of most were taken to give an approximate indication of their relative sizes.

In a small series of male and female crania, the approximate size of the diastema between C and P^1 was found to be 2.75 mm, between P^1 and P^2—1.90 mm, between P^2 and P^3—0.35 mm; P^3 lies close up against M^1. The lengths of these diastemata vary quite considerably (C to P^1, 2.2–3.5 mm; P^1 to P^2, 1.2–2.8 mm; P^2 to P^3, 0.1–0.5 mm), but C to P^1 is always greater than P^1 to P^2, and P^2 to P^3 is invariably the smallest by far in each of the individuals examined. The differences between male and female diastemata in this small series did not appear to be significant.

The anterior three upper molars all follow the same basic pattern (plate 17). Each consists of four main cusps situated on the lingual half of the tooth and four buccal cusps derived from the external cingulum. The names of these cusps (following the terminology of Gregory, 1922) are (fig. 6):—

Four main cusps: mesiolingual, protocone; distolingual, hypocone; mesiocentral, paracone; distocentral, metacone.

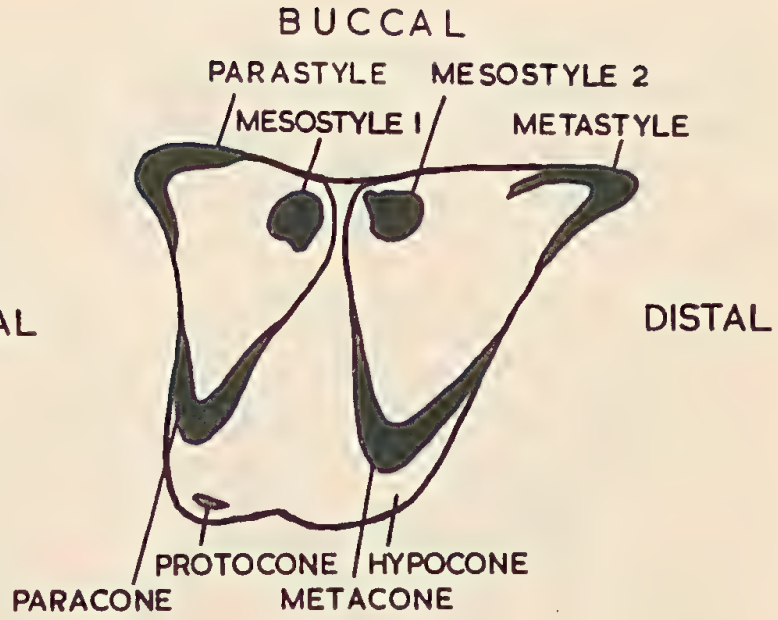

Fig. 6.—Diagram of the cusp arrangement in a typical *P. nasuta* upper molar (left M^3).

(Gregory suggests that the "hypocone" may be a true hypocone as derived in placentals, or an extension of the metaconule).

Four buccal cingulum cusps: (from mesial to distal) parastyle, mesostyle 1, mesostyle 2, metastyle.

(In his drawings on page 72, Gregory has labelled the posterior four teeth of *Perameles* as P4, M1, M2, and M3, instead of M1 to M4). In shape, the first three upper molars are roughly trapezoidal, with the mesiodistal dimension longer buccally than lingually and the lingual and buccal surfaces more or less parallel. The buccal part of the occlusal surface of each molar projects ventrally more than the lingual part, but, as the alveolar margin projects ventrally far more on the buccal than on the lingual side, it is the lingual part of each molar which is the more hypsodont. M^1, M^2, and M^3 each show two raised triangular areas, the bases of which lie along the buccal border of the tooth and the apices of which point lingually. The bases are thus formed by the cingulum cusps and the apices by the large V-shaped paracones and metacones. Each mesial triangle consists of the paracone lingually and the parastyle and mesostyle 1 at the mesial and distal ends of the base on the buccal side; each distal triangle is formed by the metacone lingually and mesostyle 2 and the metastyle at the mesial and distal ends of the base on the buccal side. The metacone is larger than the paracone and, in general, the cusps of the distal triangle are larger than those of the mesial triangle. Compared with the distal triangle, the mesial triangle is particularly small in M^1, relatively less so in M^2 and the difference is still less marked in M^3. On the lingual side of each molar, there is a narrow platform, well below the level of the tips of the paracone and metacone. On the lingual edge of this platform, the weakly developed protocone (mesially) and the still weaker developed hypocone (distally) are situated. This lingual platform is extended buccally to fill the gap between the mesial and distal triangles of each molar. M^4 is built on the same basic pattern as M^1–M^3, but it is considerably reduced, mainly distally. The mesial triangle of the tooth is intact and has a particularly large paracone, but mesostyle 1 is rather small; of the distal triangle, only a single cusp remains. Bensley (1903) working on *P. doreyana* (= *Echymipera doryana*) suggests that the reduction of the distal part is due to the lack of development of the metacone. If this is so, the remaining distal cusps would be mesostyle 2 or the metastyle, but it would seem that

the homology of this cusp is best considered uncertain. Of the two lingual cusps of M^4, the protocone is present and well developed, but the hypocone appears to be consistently absent. All four of the upper molars have three roots, two situated buccally and a larger, single, lingual root. The adjacent surfaces of M^1–M^4 are in close contact with one another buccally, but lingually they are well separated. There is thus a triangular gap (base lingually) between the adjacent mesial and distal ends of the upper molars (plate 17).

(2) *Lower teeth:* The lower incisors, are all fairly large teeth and, especially the mesial two pairs, markedly procumbent (plate 19). The buccal (labial) surface of the crown of I_1 and I_2 are high, thickly enamel-covered and have sharp incisal edges. In I_3, the buccal surface is also enamel-covered, but the incisal edge, and in fact the whole of the incisal half of the crown, is bifid, the mesial portion being about double the size of the distal. There is a small diastema between the mesial incisors, but the other adjacent surfaces of the incisors lie close together or touch. Viewed from the occlusal surface, the mesial and distal surfaces of each of the three incisors converge lingually from the incisal edge towards the base of the crown. Because of the marked procumbency of the teeth, a small amount of what should probably be termed root is then usually also seen on I_1 and I_2 before these teeth enter their alveoli. All of the incisors have extremely long roots which run back posteroventrally from the crown into the mandible. On the external surface of the mandible, a substantial portion of the roots of the incisors are generally exposed, due to the thin, outer, bony walls of the alveoli having been resorbed or lost.

The male and female $\overline{C}$ teeth are each similar in structure and size to their upper equivalents. The base of the crown of the male $\overline{C}$ is large, mainly due to its considerable mesiodistal length. The crown is generally buccolingually flattened and the mesial and distal edges curve gradually and evenly up from the base until they meet at the incisal tip. Approximately the incisal 1/3 of the tooth is enamel-covered, on both the buccal and lingual surfaces. As it emerges from its alveolus, the female $\overline{C}$ is far smaller than the male equivalent (see Part II), but, like the male $\overline{C}$, it is also buccolingually flattened. From the base upwards, the mesial and distal edges run roughly parallel for a short distance, but they then converge rapidly to a point, a small distal cuspule marking the junction of the two portions. In the female, the incisal half of the tooth is enamel-covered, both lingually and buccally. In both sexes, the $\overline{C}$ teeth lean buccally to the extent of about 45° from the vertical. The $\overline{C}$ is separated in both sexes by large diastemata from I_3 and P_1; the size of the former diastema is about 4.75 mm, and the latter about 3.5 mm.

The three lower premolars (plate 19) are very similar in structure to their upper equivalents, except that P_3 is similar to P_1 and P_2 and does not have the extra development found on P^3. The lower premolars are all buccolingually flattened and have a large central cusp and small mesial and distal cuspules. However, in all of these teeth the distal cuspule and associated part of the tooth is considerably larger than the mesial (plate 16). In size, $P_1 < P_2 < P_3$. P_1 is separated from P_2 by a diastema of about 1.25 mm, on average; P_2 lies close to P_3, but a very small gap can usually be seen; P_3 lies close to, and often actually abuts against, M_1. Each lower premolar has subequal, buccolingually-flattened mesial and distal roots. The bony processes described between the roots of the individual and adjacent upper premolars are also present between the lower premolars.

The four lower molars are each relatively more elongated than their upper equivalents in the mesiodistal direction and do not have any cingulum cusps such as are found in the upper molars (plate 19). In addition, the lower molars are hypsodont teeth both lingually and buccally. All four lower molars have a similar cusp arrangement, but in M_4 the distal portion of the tooth is considerably reduced, although not relatively as much as M^4. The names of the cusps of the lower molars, again following Gregory (1922) are (fig. 7):—

Buccal (mesial to distal): protoconid, hypoconid.

Lingual (mesial to distal): paraconid, metaconid, entoconid, hypoconulid.

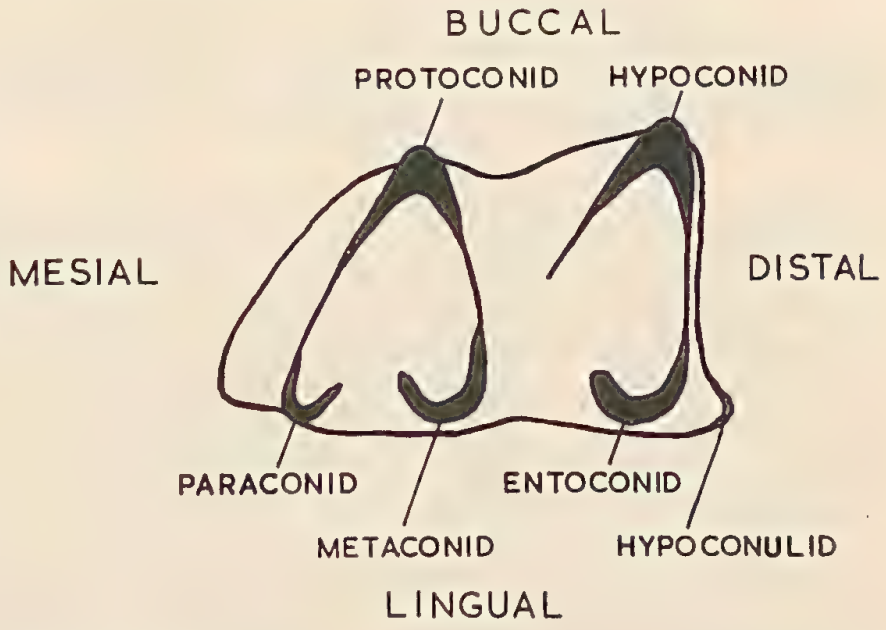

Fig. 7.—Diagram of the cusp arrangement in a typical *P. nasuta* lower molar (right M_3).

The cusps on the lower molars (plate 19) show a similar arrangement to that seen in the upper molars in that they are also arranged to form mesial and distal triangles on each tooth, but in the lower molars, the bases are on the lingual instead of the buccal sides of each tooth and, in addition, there are certain other differences. The apex of the mesial triangle is formed buccally by the large, V-shaped protoconid; lingually, the small paraconid (mesially) and the large metaconid (distally) form the base. The apex of the distal triangle is formed by the large V-shaped hypoconid on the buccal side. On the lingual side, the fairly large entoconid lies almost directly lingual to the hypoconid and forms the distolingual corner of the base, but there is no cusp to complete the mesiolingual corner of the triangle. A very small additional cusp, the hypoconulid, is found on the extreme distolingual corner of M_1–M_3. It forms a small backward extension of the distolingual corner of the tooth, but does not take part in the formation of the distal triangle. In M_1 to M_3 the distal triangle is the larger, but as one proceeds from M_1 to M_3 the mesial triangle becomes more nearly equal to the distal triangle in each tooth. In M_4 the distal triangle is very greatly reduced and is only a small fraction of the size of the triangles in any of the other lower molars. In M_1–M_3 there is only a trace of the flat platform described between the mesial and distal triangles of the upper molars; in M_4 the platform is better developed because of the great reduction of the distal triangle. On the mesial ends of M_2, M_3 and M_4 a fairly prominent shelf is developed from the cingulum. The shelf gets progressively larger from M_2 to M_4 where it is particularly well developed. Each lower molar has a mesial and a distal root, each of considerable length and subequal in size.

(3) *Eruption sequence:* Material available from the present study only allows assessment of the relative eruption times of the last four teeth—the last premolar and the last three molars. In the youngest specimens available, the incisors, canines, P1, P2, dp3, and M1 are all present. The canines are only about half erupted, but the other teeth are all fully out. M2 is the next tooth to erupt and it is followed by M3. Finally M4 erupts and, at about the same time, P3 replaces dp3. The canines, particularly in the males, may not be fully erupted, even after P3 and M4 are fully out. The lower teeth all appear to erupt in advance of their upper equivalents. The incisors, canines, and premolars lie close together when they first erupt and the various diastemata described above open up as the cranium and mandible elongate.

From the material studied by Wilson and Hill (1897) it is clear that the first tooth to erupt in *P. nasuta* is dp3, lower tooth first. The incisors follow (again lower teeth first); the canines, P1, P2, and M1 follow closely behind the incisors and may even start erupting at about the same time as those teeth.

Kingsmill (1962) gives some indications as to the age at which the various teeth erupt. At 48 days, the age of the youngest specimen examined, dp3, the incisors, canines, P1, P2, M1, M2, and M_3 project above the bone. At 61 days, dp3 can be seen above the gum and these teeth are not shed before 137–361 days. Most of the permanent teeth are visible above the gum in the period between 48 and 61 days, but M^3 and M_4 do not appear until 61–126 days and M^4 not until about 137 days. P3 appears above the alveolar margin at 61 to 126 days, but was "still embedded in the gum" till 137–361 days. These figures were based on only five specimens, but they do give some rough indication of eruption times.

(4) *Occlusion and attrition:* The dentition of *P. nasuta* is adapted to an omnivorous, mainly insectivorous, type of diet, but, to quote Gregory (1922), with "incipient adaptation towards a grinding type of molars". When the fully closed jaws are examined in a prepared skull (plate 20), or a formalin preserved whole specimen, four most significant features of occlusion can be seen:

(a) The lower incisors lie considerably lingual to, and do not directly occlude with, the upper incisors. Although this is the case when the jaws are in the fully closed position, during biting or chewing, a slight amount of unilateral movement at the mandibular condyles would allow the upper incisors (I^2–I^4) of the left or right side to bite into the occlusal surfaces of the lower incisors (I_1–I_3) of the same side. This slight amount of movement should be possible at the condyles although, according to Abbie (1939), the temporo-mandibular joint of *Perameles* does not include an intra-articular disc. Examination of the occlusal surfaces of the lower incisors shows mesiodistally oriented facets which could be the result of attrition by the incisal edges of I^2–I^4. The worn shape of the incisal edges of the upper incisors appear to confirm this type of usage. Each takes the form of a blunt point, with a very long mesio-ventrally directed portion which would occlude with the occlusal surface of the lower incisors, followed by a short, distoventrally directed section, possibly the result of wear by the incisal edges of the lower incisors in passing buccally or lingually in the unilateral movement postulated above.

(b) I^5, the upper and lower canines and all of the premolars, alternate (starting mesially with I^5, and lower and upper teeth then alternating). Together, these teeth form a very efficient grasping and holding mechanism.

(c) The upper molars overhang the lower considerably buccally. As a result, the buccal cingulum cusps of the upper molars do not directly occlude with any part of the lower molars in the resting position. In any lateral chewing movements, with the jaws slightly open, they do however offer an increased grinding surface for the lower molars to work on.

(d) The mesial and the distal triangles of the upper and lower molars interdigitate, the distal triangle of the lower molar occluding between the mesial and distal triangles of its upper equivalent. The mesial triangle of M_1 occludes between the mesial triangle of M^1 and the distal part of P^3. This arrangement would function particularly well in a chopping type of action.

With regard to attrition, the deciduous premolars develop an occlusal concavity, with the mesial portion higher than the distal. This wear must be caused indirectly by food (probably including some sand), as the upper and lower deciduous premolars cease to occlude at a very early age whilst the animal is still suckling.

Wear of the incisors was dealt with above, under occlusion; wear on the canines is in almost all cases only slight and generalised. Viewed from the lateral surface, the premolars form an efficient, interlocking series of triangles and the distal edges of the lower premolars wear against the mesial edges of the upper. Reciprocally shaped facets, usually approximately straight, are worn.

In the upper molars, the mesial triangle shows signs of wear before the distal triangle and the lingual part of each tooth wears before the buccal portion. Correspondingly in the lower molars, the distal triangle and the buccal half of the tooth show wear sooner. Very little wear at all occurs on the buccal cingulum cusps of the upper molars. The relative amount of wear on each molar in the toothrow of an individual follows the eruption sequence M1 to M4. Resorption of alveolar bone was noted in a number of older specimens in the premolar-molar region. In these individuals, the coronal halves of the roots of the premolars and molars were often exposed above the resorbed alveolar margin and the remaining portions of the sockets were eroded, often to twice their natural diameter.

THE ANATOMY OF THE SKULL AND TEETH OF P. GUNNII

The anatomy of the skull and teeth of *P. gunnii* is very similar to that of *P. nasuta*. However, in general, the skull of *P. gunnii* is smaller and more delicately built than that of *P. nasuta* and, in addition, there are a few features in which there are clear-cut anatomical differences between the two species.

(a) *Cranium* (Plates 21 and 22).

(1) The temporal lines in *P. gunnii* are quite well developed, but they remain widely separated (6 to 9 mm apart) right up to the lambdoid crests and thus do not form a sagittal crest posteriorly.

(2) The lambdoid crests are much smaller and less rugged than in *P. nasuta*.

(3) Partly as a result of (1) and (2) above, the posterior part of the dorsal surface of the calvaria is flattened, low, and rounded in *P. gunnii*. Also, the most posteriorly projecting region of the cranium in *P. gunnii* is the central portion of the occipital bone, and not the lambdoid crests as in *P. nasuta*.

(4) Viewed from above, the minimum diameter of the cranium between the orbits is considerably greater in *P. gunnii* than in *P. nasuta.*

(5) The alisphenoid bullae and the tympanic bones of *P. gunnii* are larger than those in *P. nasuta.*

(6) The height of the foramen magnum of *P. gunnii* is relatively slightly less than in *P. nasuta* and hence the foramen is generally more oval-shaped.

(7) In addition to anterior and posterior palatal vacuities, similar to those seen in *P. nasuta,* certain additional areas of the palate are typically missing in *P. gunnii.* (i) One or two anteroposteriorly elongated pairs of vacuities are found between the anterior and posterior palatal vacuities; and (ii) random fenestration occurs in most of the palate posterior to the posterior palatal vacuities. The posterior palatal vacuities are generally larger in *P. gunnii* than in *P. nasuta* and almost invariably lack a median partition.

(b) *Mandible:* The mandible of *P. gunnii* is considerably more slender than that of *P. nasuta* and the relative narrowness of the anteroposterior dimension of its ascending ramus is particularly striking. Compared to *P. nasuta,* the coronoid process of *P. gunnii* is usually relatively higher, anteroposteriorly shorter, and its tip tends to be directed posteriorly more frequently. The mandibular notch is relatively deeper in *P. gunnii* than in *P. nasuta.*

(c) *Dentition* (plates 21 and 22): There are two major differences between the dentitions of *P. gunnii* and *P. nasuta:*

(1) The crown of I^5 in *P. gunnii* (plate 23) is mesiodistally long, buccolingually flattened and bears more resemblance to a small *Perameles* premolar than to the caniniform-shaped I^5 of *P. nasuta.* In addition, this tooth is two-rooted in *P. gunnii,* whereas the equivalent tooth in *P. nasuta* has only a single root.

(2) In *P. gunnii* the male canine is only slightly larger than that of the female, and much smaller than the equivalent tooth in *P. nasuta.* The same anatomical differences are present between the male and female canines in *P. gunnii* as were described for *P. nasuta,* but they are not as clearcut in *P. gunnii* and, on occasions, sexing by means of the canines only can be extremely difficult.

Other than on the above two points, the dentitions appear to be very similar, although there is a suggestion that the shapes of the incisal edges of I^2–I^4 may differ slightly in the two species (in *P. gunnii* the distal part seems to be longer than in *P. nasuta* and to end in a minute cuspule) and also that the protocone in the upper molars might be relatively slightly larger in *P. gunnii* than in *P. nasuta.*

THE ANATOMY OF THE SKULL AND TEETH OF THE P. BOUGAINVILLE GROUP

The skulls and teeth of *P. nasuta* and *P. gunnii* are of approximately similar size, but readily distinguishable on the anatomical differences discussed under *P. gunnii* above. All of the other *Perameles* skulls studied are of considerably smaller size and have initially been included together in this *P. bougainville* group.

(a) *Cranium* (plates 21 and 22): The *bougainville* group of crania, in addition to being considerably smaller, differs from *P. nasuta* and *P. gunnii* in the following respects:

(1) Viewed from above or below, the muzzle of the *P. bougainville* group appears to taper more sharply from P^2 forwards; in lateral view, the profile of the dorsal surface of the muzzle shows a slight concavity (mainly at about the region of the fronto-nasal suture). In *P. nasuta* the muzzle profile is flat or even slightly convex; in *P. gunnii* it is usually also flat, but there may occasionally be a very slight concavity.

(2) In the *P. bougainville* group the maxillary fossa, on the lateral side of the maxilla above the posterior molars, appears deeper than in *P. nasuta* or *P. gunnii*, although rarely the fossa may be quite marked in the latter species.

(3) The lacrimal bones in the *P. bougainville* group are prominent and similar in form to those of *P. gunnii*, which stand out slightly more than those of *P. nasuta*.

(4) The palatal vacuities of the *P. bougainville* group are similar to those found in *P. gunnii* and far more extensive than those of *P. nasuta*.

(5) In their weakly developed lambdoid crests and in the absence of sagittal crests, the *P. bougainville* group also resembles *P. gunnii*.

(6) The alisphenoid bulla takes two clearly different forms (plate 22) in the *P. bougainville* group. (i) In the Dorre and Bernier Island specimens, the bulla is of a similar order of size to those of *P. nasuta* and *P. gunnii*, although it is relatively slightly larger than even that of *P. gunnii*. (ii) In all of the rest of the specimens (with one possible exception discussed below) the bullae are all extremely large and more similar in relative size to the bullae found in the genus *Isoödon*.

(b) *Mandible:* No important differences, except size, are apparent in the mandible. The pattern is basically like that of *P. gunnii*.

(c) *Dentition* (plates 21 and 22):

(1) The deciduous premolar is relatively and absolutely larger and generally better developed in the *P. bougainville* group than in either of the two larger species.

(2) The upper molars of the *P. bougainville* group usually appear to have better developed mesiolingual cusps (protocones) than *P. nasuta* and *P. gunnii*.

(3) Sexual dimorphism was not apparent in the canines of this group.

(4) The crown of I^5 may be either caniniform, as in *P. nasuta*, or it may be elongated mesiodistally and resemble that of *P. gunnii*. In thirty-four out of the thirty-five specimens with caniniform crowns, I^5 was single-rooted; in three out of the five specimens with mesiodistally elongated crowns, I^5 was double-rooted. However, because of their small size, the roots are not easy to identify, even when x-rays are used, and the three discordant cases might well be considered uncertain. The long I^5 is always found in the Dorre and Bernier Island specimens, whilst, with one exception, the rest all have caniniform I^5 teeth.

DISCUSSION

The anatomical differences in the skull and teeth between *P. nasuta* and *P. gunnii* are straightforward and call for little additional comment. The two species can be readily distinguished on a number of anatomical points, particularly on I^5, the canines and the palatal vacuities, and hence clearly merit specific separation.

From the foregoing outline of the anatomy of the skull and teeth of the *P. bougainville* group, except for the considerable difference in size, it is apparent that these specimens are very similar to *P. gunnii* in most features examined. The material included in this *P. bougainville* group all come from the western half of Australia, but were listed under "Material" in three subsections. The basis for this subdivision can now be discussed.

The specimens in subsection (1), twelve plus one from south-western South Australia and three plus one from south-eastern Western Australia, all have mesiodistally short (crown length 0.9–1.0 mm), single-rooted I^5 teeth, and large alisphenoid bullae. These specimens come from an area from which *P. myosura notina* and *P. bougainville notina* were described by Iredale and Troughton (1934) and Marlow (1962) respectively. The sixteen (?) specimens from South Australia have the same characteristics and are anatomically indistinguishable from specimens of subsection (1).

The specimens in subsection (2), the five specimens from Dorre and Bernier Islands, all have mesiodistally long (crown length 1.1–1.3 mm) I^5 teeth and small alisphenoid bullae. Three out of five of these I^5 teeth have double roots and the other two are probably single, but mesiodistally long. These specimens come from the localities from which *P. bougainville* and *P. bougainville bougainville* were described by Iredale and Troughton (1934) and Marlow (1962) respectively.

The five specimens in subsection (3) are thinly scattered in the western part of central Australia, the region from which the species *P. eremiana* has been described. I^5 is absent in one specimen, but three out of the four remaining specimens have small, single-rooted I^5 teeth, while the fourth specimen has a long, double-rooted I^5 tooth. Further, in three out of the four specimens in which the relevant feature is undamaged, the alisphenoid bullae are large; the fourth specimen is not fully adult, but the bulla appears to be of the small type. This group of specimens from central Australia is very small, not all are adult, some are damaged and the localities ascribed to most of them are rather vague. It would seem unwise at this stage to use the above information to comment on skull and tooth features of this species.

From the above analysis of the small forms of *Perameles*, it would seem that, at least for the time being, Tate's suggestion (1948) of the close inter-relationship between the small, long-nosed bandicoots should be followed and that, for reasons of priority, Marlow's terminology (1962) of *P. bougainville bougainville* for the Dorre and Bernier Island form and *P. bougainville notina* for the South Australian form should be used. However, the two clearcut differences in the skull and teeth found between these two forms suggest the possibility that, on further investigation, specific separation might be warranted. Material of *P. bougainville myosura* and *P. fasciata*, and features other than the anatomy of the skull and teeth, will clearly have to be considered before the intrageneric taxonomy of *Perameles* can be fully resolved.

SUMMARY

(1) The anatomy of the skull and teeth of *P. nasuta* has been described.

(2) Anatomical variations in the skull and teeth between certain species of *Perameles* have been recorded.

(3) Clear anatomical differences in certain of the above features separate the two large eastern species (*P. nasuta* and *P. gunnii*) and also two of the small western forms (*P. bougainville bougainville* and *P. bougainville notina*).

ACKNOWLEDGEMENTS

I should like to thank Mr P. L. Davies, Department of Anatomy, University of Sydney, and Mr B. J. Marlow, The Australian Museum, Sydney, for discussions on various aspects of this paper. Mr G. L. Williams, Department of Anatomy, University of Sydney, took the photographs which illustrate this paper.

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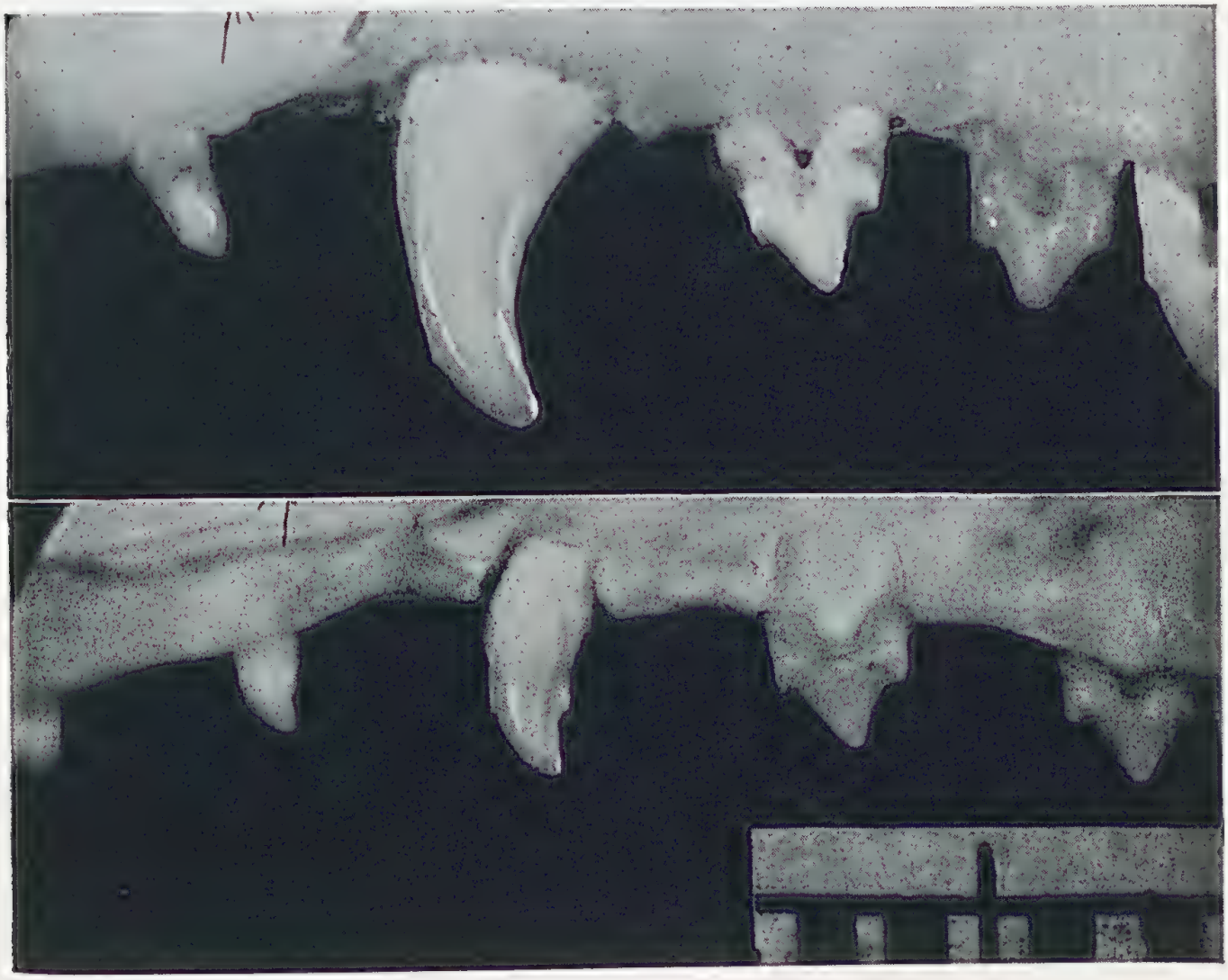
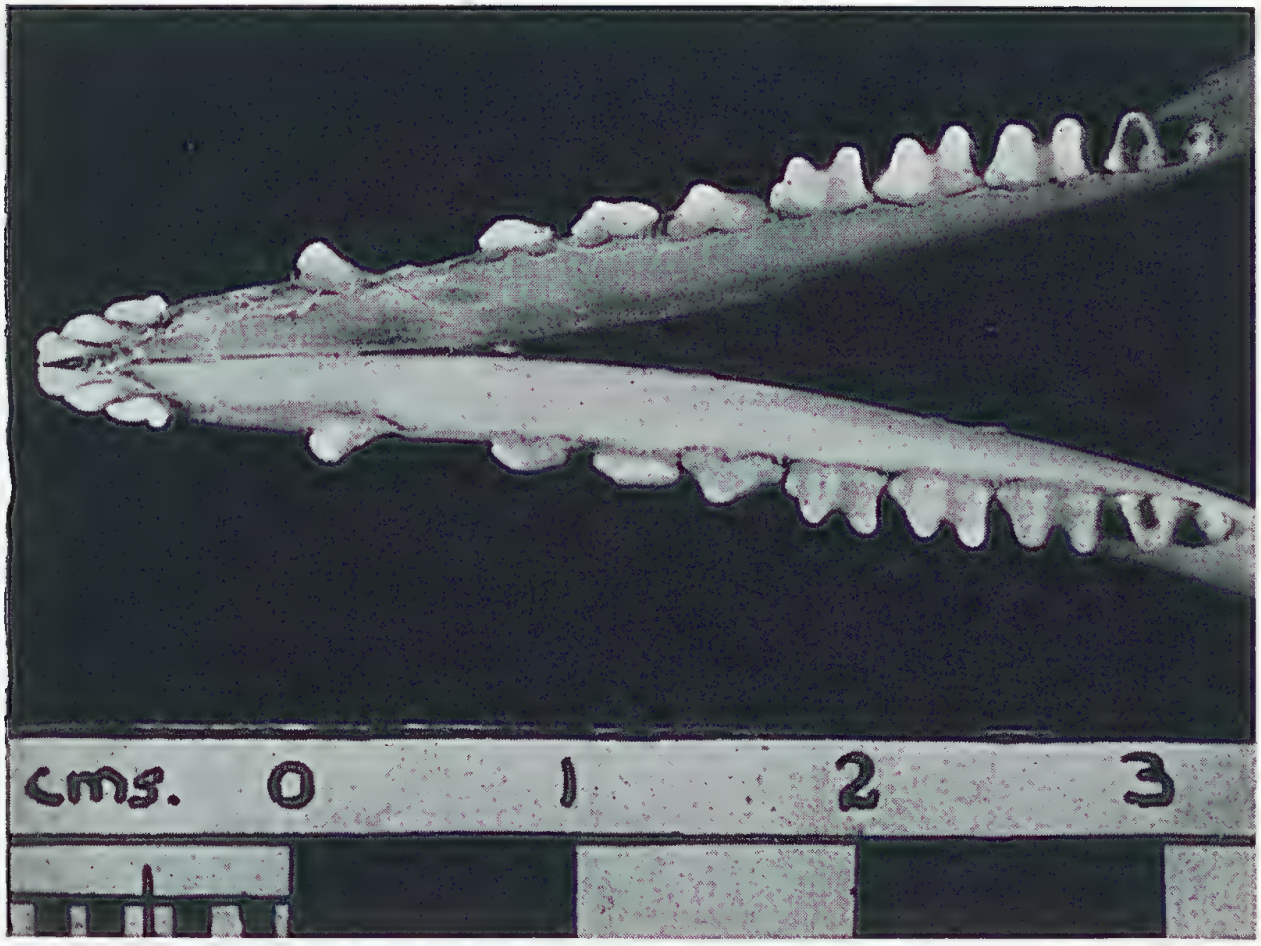
Plate 16 (above): *P. nasuta* female (P.5), lateral view of the skull, teeth and mandible.

Plate 17 (below): *P. nasuta* female (P.5), occlusal view of the upper teeth.



P. nasuta, male (M.8231), above, and female (M.8310), below. Lateral view of I^5–P^2. (C–P^1 diastema unusually small in male).

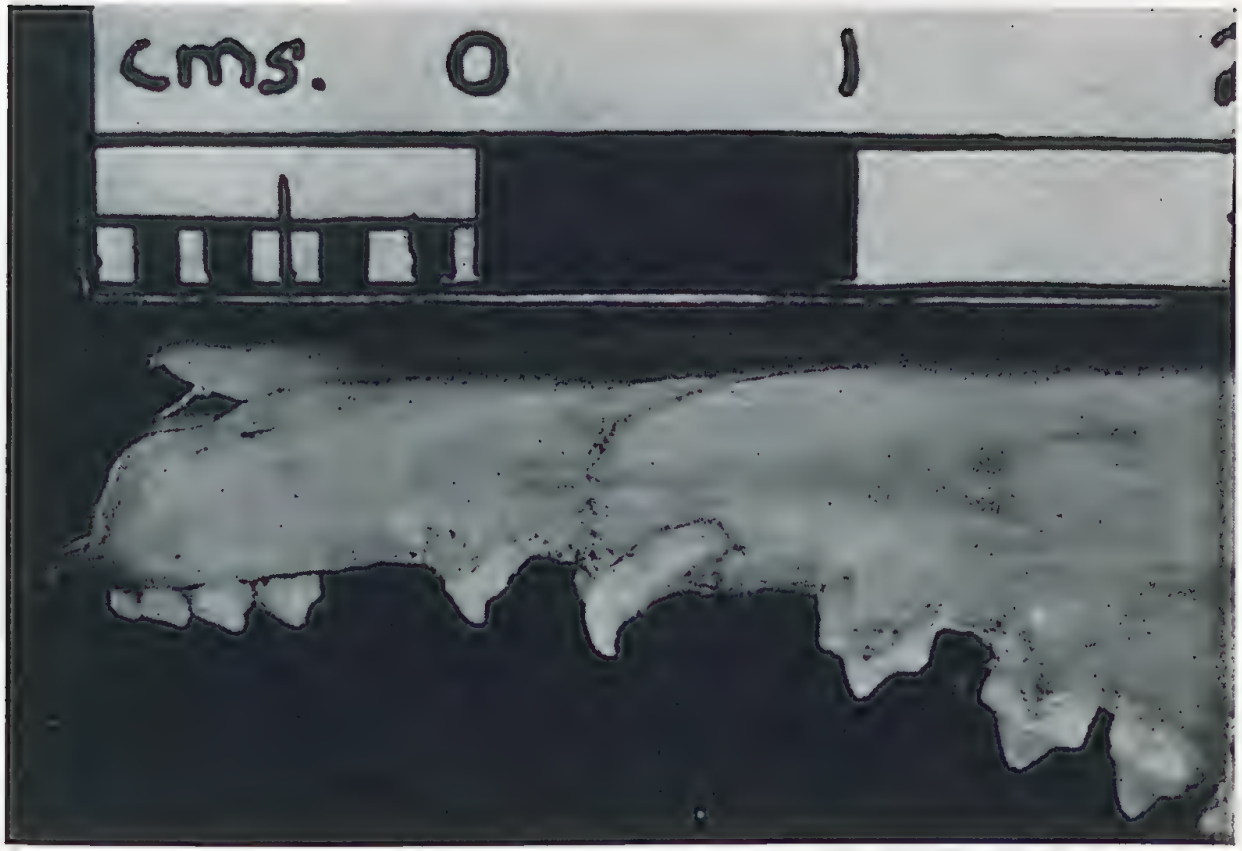


P. nasuta female (P.5), occlusal view of the lower teeth

P. nasuta female (P.5), ventrolateral view of the occluded teeth

Crania, lateral views. From above downwards: *P. nasuta* male (M.8231); *P. gunnii* male (X.428); Dorre Island Western Australia, male (10576); Fisher, South Australia, sex unknown (M.2086).

Crania, ventral views. From above downwards: *P. nasuta* male (M.8231); *P. gunnii* male (X.428); Dorre Island, Western Australia, male (10576); Fisher, South Australia, sex unknown (M.2986).



P. gunnii female (MM.2), lateral view of anterior upper teeth

A NEW SPECIES OF *ATTENUATELLA* (BRACHIOPODA) FROM PERMIAN BEDS NEAR DRAKE, NEW SOUTH WALES

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Plate 24. Text Figs 1-3 Manuscript received, 10th August, 1965

Abstract

A new species *Attenuatella multispinosa* is described from the mid-Permian Gilgurry Mudstone at the top of the Boorook Group, near Drake, northern New South Wales.

Introduction

Attenuatella is a small spinose Permian brachiopod genus allied to *Crurithyris*. Proposed for American species by Stehli (1954), it has also been described from Russia by Chernjak (1963), New Zealand by Waterhouse (1964) and recently found in New Caledonia by Messrs Noesmoen and Espirat, and the writer. This paper describes the first species to be identified in Australia: it was noticed early in 1965 by the writer in a collection at the Australian Museum and the specimens have been borrowed and described with the kind permission of Mr H. O. Fletcher, Deputy Director of the Australian Museum.

SYSTEMATIC DESCRIPTION

Genus **Attenuatella** Stehli 1954

Type species: Attenuatella texana Stehli (1954).

Diagnosis: Small brachythyrid species with inflated elongated ventral valve and almost flat dorsal valve, ventral umbo incurved, ventral interarea high, delthyrium open, dorsal interarea low, vertical to commissure. Shallow ventral sulcus, dorsal fold in some forms. Some species costate and all ornamented by fine erect hollow spines in concentric rows. Interior of ventral valve has stubby teeth, short umbonal callosity, long median elevation on which muscle scars are sited. Dorsal valve with large cardinal process, sessile socket and crural plates, large crura, spire, tiny median septum in some species, two narrow elongated impressions or ridges close to mid-line, and two larger rounded impressions laterally. Shell impunctate.

Discussion: Internal features of the dorsal valve in the diagnosis are based on a New Zealand species *A. incurvata* Waterhouse (1964) and a Russian species *A. stringocephaloides* Chernychev and Liharev in Liharev and Einor (1938). The ventral valve of the Australian form is unusual in that a low ridge lies each side of the muscle field, probably because the muscle field is deeply impressed.

Attenuatella multispinosa sp. nov.

Pl. 24. Text figs. 1-3.

Material: An internal and external mould of two dorsal valves and about a dozen ventral valves, several distorted, and all preserved as natural internal and external moulds.

Locality: Gilgurry Mudstone, Boorook Group, between Sandy Hill and Drake, near Crooked Creek, northern New South Wales.

Diagnosis: Elongated moderately inflated *Attenuatella* with shallow ventral sulcus, faint dorsal costae, and fine spines (14-18 per millimetre). Well developed ridges enclose the ventral muscle field laterally. Crural plates low.

Holotype: F 42104, pl. 24 (figs 5, 6) Australian Museum.

Paratypes: F 42100-3, 42105, 51522-26. Australian Museum.

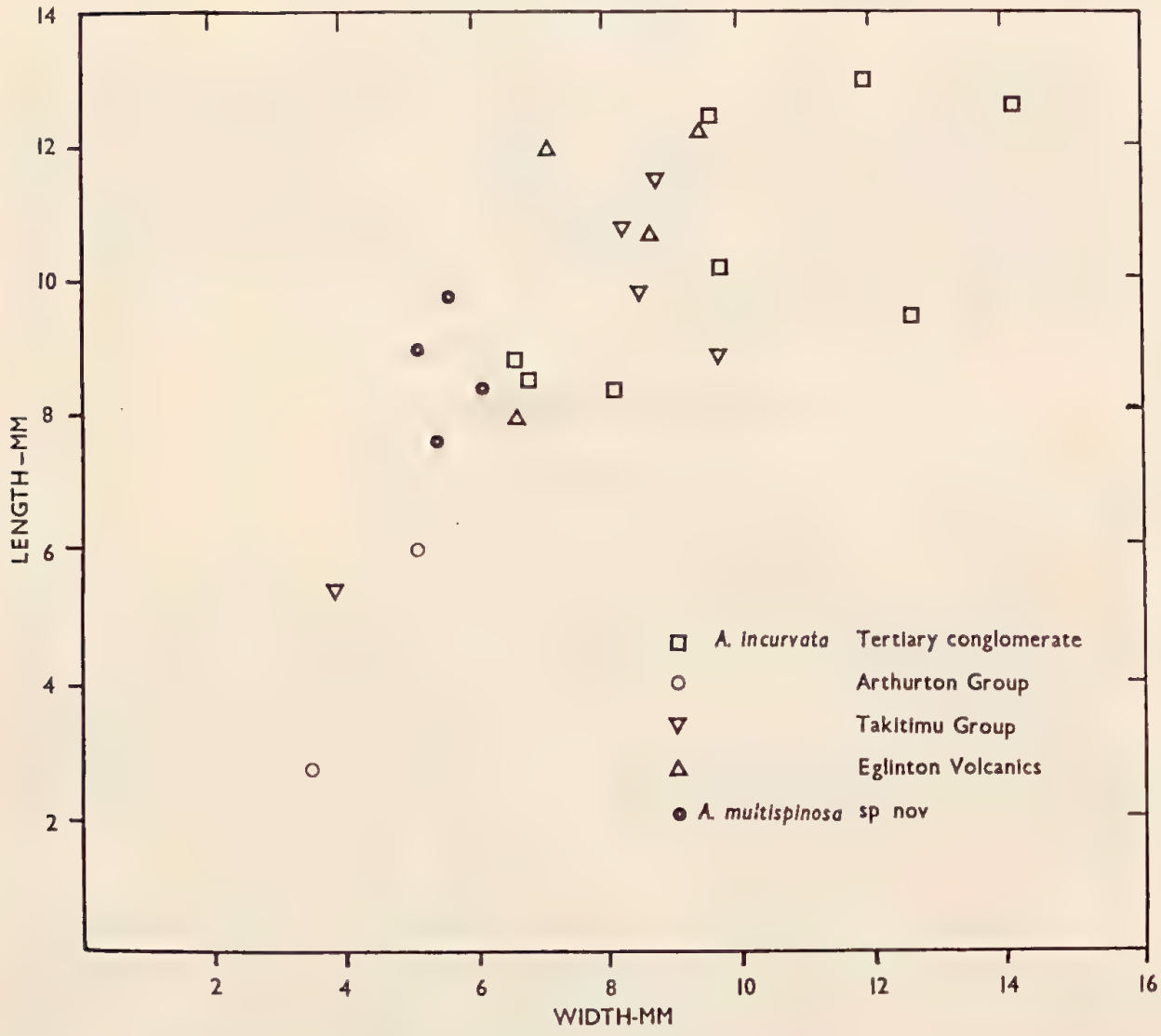

Fig. 1—Graph of length and width of ventral valves (in millimetres) for Australian and New Zealand *Attenuatella*

Measurements (*in mm*) Ventral Valve.

Specimen	Width	Length	Height	Hinge Width	Umbonal Angle	Width Ventral Muscle Field	M^1
F42100* ..	?5	9	3	..	..	0.8	5·5
F42102* ..	5·5	9·9	2.8	?4·5	70°	1·3	5·5
F42105* ..	5·3	7.6	2.3	?4.6	75°	1·4	4.6
F42104 ..	6.3	8.1	3.6	?4.7	60°	..	5·2
Dorsal Valve							
F51524 ..	3·4	3	2.5				
F51522 ..	3.0	3.0	2				

* Ventral valves preserved as internal moulds but the true length is measured from the external mould. M^1 = distance from ventral umbo to position of maximum width of shell.

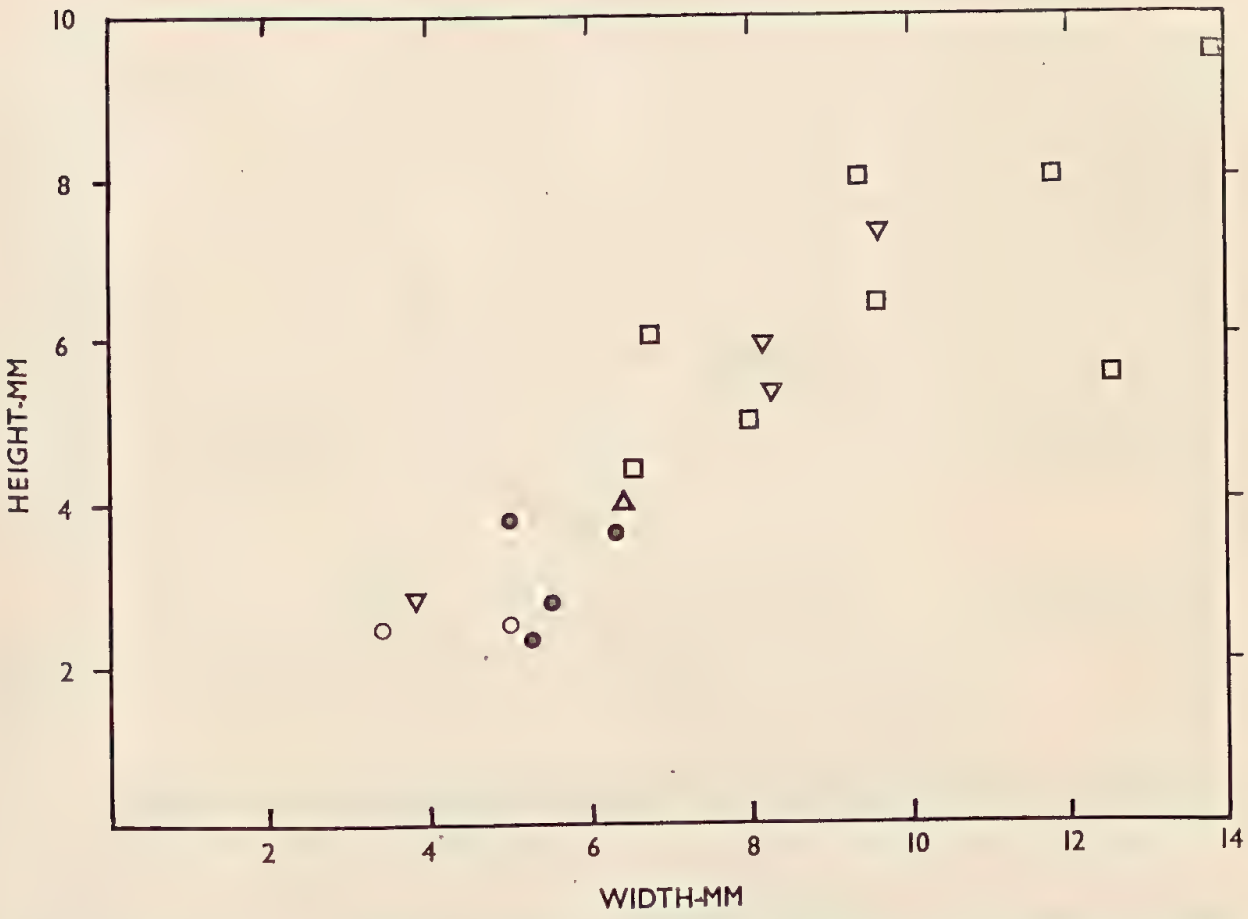

Fig. 2—Graph of height and width of ventral valves (in millimetres) for Australian and New Zealand *Attenuatella*. For legend see fig. 1

Description

External: The specimens are of medium size for the genus, with an elongate moderately arched ventral valve and an almost flat dorsal valve. The ventral umbo is extended and incurved, with posterior walls diverging anteriorly at 40 degrees to 50 degrees and the maximum width lying a little in front of mid-length. The dorsal valve is convex over the nepionic region for a width of nearly 1.5 mm and is gently concave in front. Cardinal extremities are obtuse, measuring 120 degrees to 130 degrees. The ventral interarea is high and incurved, and the dorsal interarea low and almost perpendicular to the commissure, but neither are well exposed. A narrow sulcus extends for the full length of the ventral valve and there is possibly a low fold anteriorly on the dorsal valve F42103 and a sulcus in F51522. Faint costae with wide interspaces are present anteriorly on the dorsal valves, about 14 occurring in F51522, about 7 per millimetre. Erect spines with hollow cores arise along somewhat irregular concentric rows, spaced about 12 per millimetre anteriorly in F42104 and 14 to 15 per millimetre in F42103. The spacing of spines along the row is not entirely regular, and also varies over the shell—in F51523 15 spines occur per millimetre just over 2 mm from the umbo, and spines then become very dense, over 20 per millimetre, the density gradually decreasing anteriorly. Near the anterior margin the density again increases to 18 to 19 per millimetre. In another ventral valve F51526 15 to 19 spines occur per millimetre. In the dorsal valve F51524 14 occur in 1 mm near the anterior margin, and at the anterior margin a rather irregular row has only 10 per millimetre. Growth lamellae appear at intervals of 1 to 2 mm and finer growth lines are seen only as faint traces.

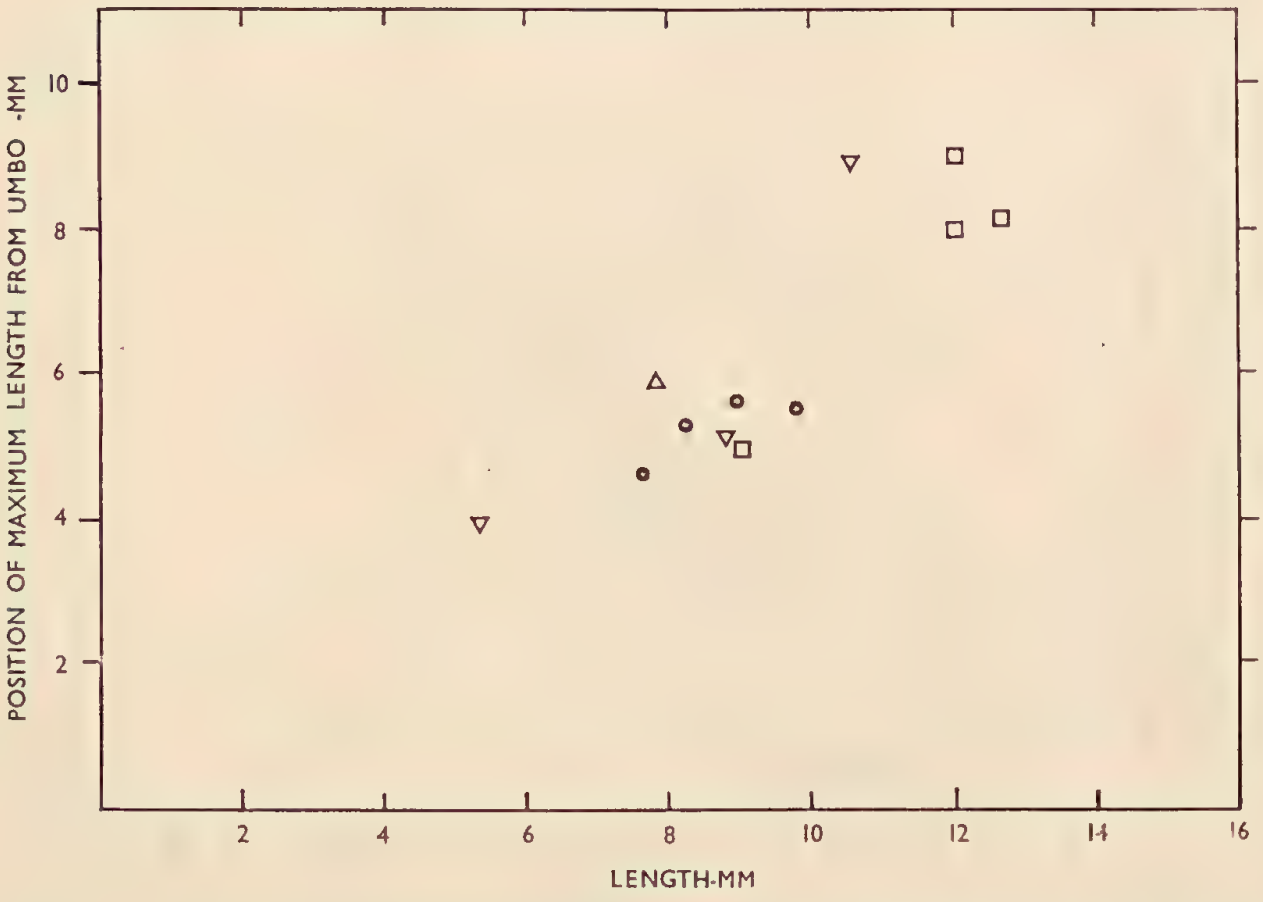

Fig. 3—Graph of dimensions (length and the position of maximum width from the ventral umbo, in millimetres) for ventral valves of Australian and New Zealand *Attenuatella*. For legend, see fig. 1

Internal: Ventral Valve. The teeth are massive and not supported by dental plates. A narrow high umbonal callosity is developed at the posterior end of a wide high median elevation which extends for two thirds to three quarters of the length of the valve. Dividing the ridge is a narrow median groove, and to each side lie a number of fine longitudinal striations which usually do not extend beyond mid-length. In F42105 the muscle ridge is concave in transverse profile with a groove each side, suggestive of adductors; in F51523 and the others the entire muscle field is convex. The muscle field is sharply depressed below the crest of the median elevation, leaving a ridge which extends for half to full length of the muscle scars, suggestive of adminicula. The remainder of the valve has fine dimples and pits.

Dorsal Valve. The dental sockets are finely denticulate in F51524 and are enclosed anteriorly by low sessile crural plates which diverge anteriorly at 115 degrees. Two blades of matrix cross the crura. Little is seen of the cardinal process: it is represented in the mould by a deep depression between the sockets; with a median posterior groove and a lobe each side. Nor are the crural supports apparent in this specimen, but they are visible in F51522 as very low plates, with erect crural bases. In front of the cardinal process lies a very short septum, less than a millimetre long, with a shallow elongated depression each side, and a larger subrounded depression lies in front to each side. The remainder of the valve is marked by fine pustules and pits.

Resemblances

Attenuatella incurvata Waterhouse (1964, pl. 20, figs 1-12; pl. 21, figs 1-9; Figs 47-52) is a slightly larger and more transverse species with a similar incurved ventral umbo and sulcus and concavo-convex dorsal valve. The spines are coarser, 10-14 occurring per millimetre. Internally the median ventral elevation is usually longer, lacks adminicular-like ridges, and has a less well-defined median groove. In the dorsal valve the dental sockets are not denticulate and the crural plates are more prominent. The holotype of *A. incurvata* and topotypes from a limestone boulder in Tertiary conglomerate have a different arrangement of muscle scars, the inner pair lying in a more anterior position. But small specimens from the Kazanian Arthurton Group, BR 929 (Waterhouse, 1964, pl. 21, fig. 8) and BR 930 (Waterhouse, 1964, pl. 21, figs 4, 7) have scars in a posterior position, similar to the arrangement in the Australian form. The position of the muscle scars in *A. incurvata* has been assumed to change with ontogeny, but this has not been confirmed because small topotypes are not known, and Arthurton specimens are sparse, small and generally poorly preserved. In the Arthurton dorsal valves the cardinal process lies in a more posterior position than in the Australian species, the socket plates are not crenulate and the crural plates are clearly visible.

Specimens recently discovered from Lower Artinskian beds of the Takitimu Group and Eglinton Volcanics of New Zealand usually have a dorsal fold and costae and a slightly lower density of spines than in *A. incurvata.* The two Takitimu specimens have no dorsal septum and a very long pair of dorsal median ridges.

Attenuatella texana Stehli (1954, pl. 25, figs 31-33) from the Lower Leonardian of Texas is known from a single ventral valve and thus cannot be compared adequately. It is similar in shape and inflation, shallow sulcus and the failure of the inner ventral ridge to reach the anterior margin. No spine density is given in the description and features of the dorsal valve are not known. Another American species *A. attenuata* (Cloud, 1944, pl. 17, figs 22-25) from the Waagenoceras zone of Las Delicias, Mexico, is more inflated with a more incurved ventral umbo. Internal details are not shown.

A. stringocephaloides (Chernyshev and Liharev in Liharev and Einor, 1938, pl. 13, fig. 5; Chernjak, 1963, pl. 42, figs 3, 4) is a more transverse shell with a wider ventral sulcus and short posterior adductor impressions (Chernjak, 1963, pl. 42, fig. 3a). *A. taimyrica* Chernjak (1963, pl. 42, figs. 5-9) is even more transverse and has a shallow ventral sulcus and inner ventral elevation that fails to reach the anterior margin.

Age

A. multispinosa comes from the Gilgurry Mudstone (Voisey, 1936, 1939, 1957), likely to be late Kungurian or early Kazanian age. The species closest to the Gilgurry form are the poorly known *A. texana* Stehli from the Lower Leonardian of Texas and Kazanian specimens assigned to *A. incurvata* from the Arthurton Group of New Zealand, but the new form is too distinctive to give any firm indication of age.

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EXPLANATION OF PLATE 24

Attenuatella multispinosa sp. nov.

x 4 approx.

Fig. 1—Internal mould of ventral valve, F42102.

Fig. 2—Internal mould of ventral valve, F42100, obliquely crushed.

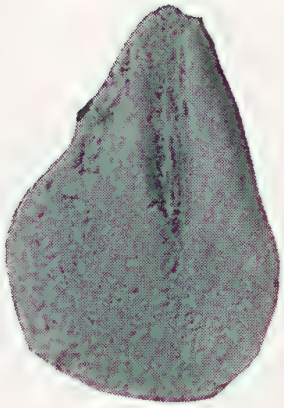
Fig. 3—Internal mould of ventral valve, F42105.

Fig. 4—Obliquely crushed internal mould of ventral valve, F51523.

Fig. 5—Lateral view of internal mould of ventral valve, F42104, holotype.

Fig. 6—Rubber latex mould of exterior of ventral valve, F42104, holotype.

Fig. 7—Internal mould of dorsal valve, F51524. This specimen seems to have been lost at the Geological Survey, only the external mould remaining.



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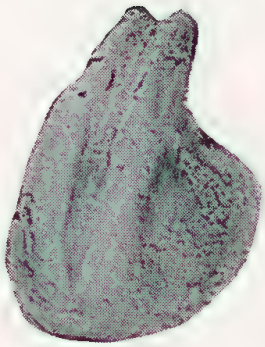

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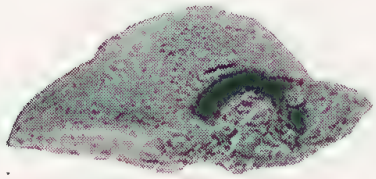

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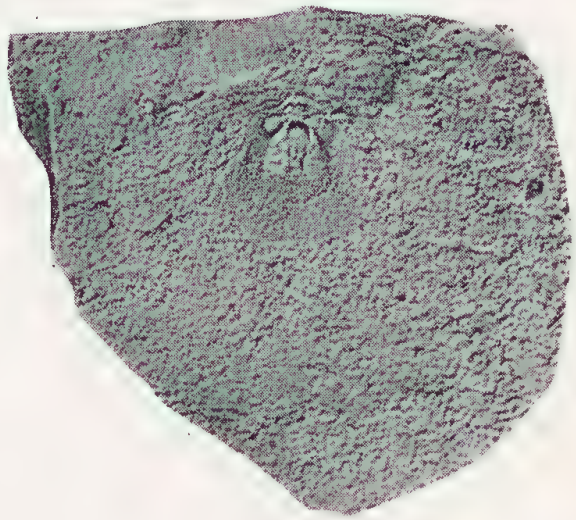

7

ON *GANGAMOPTERIS WALKOMII* SP. NOV.

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Plates 25-27. Text Fig. 1

Manuscript received, 1st July, 1965

Abstract

Gangamopteris walkomii sp. nov. is erected to contain certain small *Gangamopteris*-like leaves from the Permian of New South Wales. These leaves grew spirally on long and short shoots, and were deciduous.

Introduction

A large number of specimens bearing the proposed species were found at Duncan's Pass, Narrowneck, near Katoomba, New South Wales, by two collecting expeditions in 1949. Messrs H. O. Fletcher and R. O. Chalmers collected the specimens. From the way in which the specimens were grouped together it is probable that all were derived from the same plant. The collection is now housed at the Australian Museum, Sydney, N.S.W. All specimens bear a registered fossil number of the Museum's collection.

Gangamopteris walkomii sp. nov.

DIAGNOSIS

Leaves, obovate, becoming elliptical then rhombic at maturity; apex obtuse to rounded; leaf base narrowing gradually to a short, thick petiole; margin entire; primary venation absent in the mature leaf, secondary venation dichotomously branching and anastomosing forming elongate reticulate meshes arising from a central region of strongly developed parallel veins, or a midrib in the developing leaf; venation strongly arcuate intersecting margin in the upper third at 90 degrees, varying to less than 30 degree near petiole. Leaves arising from a closely packed spiral as tufts along a stem of unknown identity; abcission apparently occurring before the number of leaves exceeded 12 or slightly more, although leaves grew from more than one point along the stem at any one time. No stem elongation occurring after expansion of leaves of short shoots. Short shoot branching from within axil of leaf on shoot of unlimited growth. Stomata absent from adaxial leaf surface.

Type specimen: Australian Museum, F43563, the leaf as designated in the caption to fig. 7.

Paratype: Australian Museum, F43564, designated to show the long and short shoots, and habit.

Locality: Duncan's Pass, Narrow Neck, near Katoomba, New South Wales.

Horizon: Lithgow Coal Measures, of Permian age.

Specific name: The species is named in honour of Dr A. B. Walkom, of Sydney, N.S.W., palaeobotanist, and one time director of the Australian Museum, Sydney.

DESCRIPTION

Habit

A number of the specimens showed tufts of leaves attached to a branch, and in a few there was more than one tuft on a branch.

The leaves were spirally arranged, and fell leaving a small polygonal leaf scar. The average single twist of the spiral appeared to have 8 leaves. Later leaves were attached above earlier leaves where a greater number of leaves was visible. This happened commonly. The greatest number of leaves in any tuft was 12, on F43529 (fig. 2).

F43564 (fig. 8) shows a branch bearing leaves, and branching from it a small shoot bearing two tufts of leaves. The small shoot branched from within a leaf axil of the branch. Only 4 of the leaves that formed part of the leaf clump on the branch can be seen.

The medial tuft of leaves on the shoot has 5 leaves visible on the counterpart F43563 (fig. 16) and the terminal cluster has 8 leaves visible.

The shoot leaves the branch at an angle of 30 degrees, but this angle probably has been foreshortened by compression of the shoot on to the branch during burial. There is a decided bending of the shoot near the medial tuft. The longitudinal ribbing on the shoot has been distorted just below the medial tuft. This gives the impression that the shoot was straight during life. There is also a limited amount of distortion just above the medial tuft, here too, the shoot was probably straight during life. This shoot is considered to be comparable with the short shoot of a gymnosperm as there is no evidence of growth occurring at the terminal tuft.

Some stems lay across bedding planes. The stems were only ribbons of carbon when cut, e.g. specimen F43590 (not figured). There was a suggestion of a *Vertebraria*-like segmentation in these stems, e.g. the stem on F43563, reverse (fig. 16), where it is well developed, and in the largest stem of the collection F43529, reverse (fig. 20), where it is indistinct. Cross sections of stems appeared on specimen F43588, reverse (fig. 15), where they have been compressed to give stellate sections.

Leaves grew spirally along the short shoots. Specimen F43562 (fig. 9) shows that the leaves did not all grow in the same plane. This specimen shows a tuft compressed axially. The three petioles attached to cushions visible on the lower tuft of specimen F43568 (fig. 13) arose in a diagonal row typical of a closely adpressed spiral. The cushions shows a spiral arrangement on specimen F43528 (fig. 17) and less clearly on the counterpart, F43529, obverse (fig. 2). Where leaf scars are visible, neighbouring attached leaves are generally elliptical.

The petiole expanded markedly just above the abcission layer into a rounded, almost triangular cushion. This shows best in the three lower petioles shown on fig. 13 (specimen F43568). There is no evidence to suggest any form of sheath, stipule or scale grew at the base of the leaf. Scars are absent from most stems, or if present are found only just below a tuft of leaves.

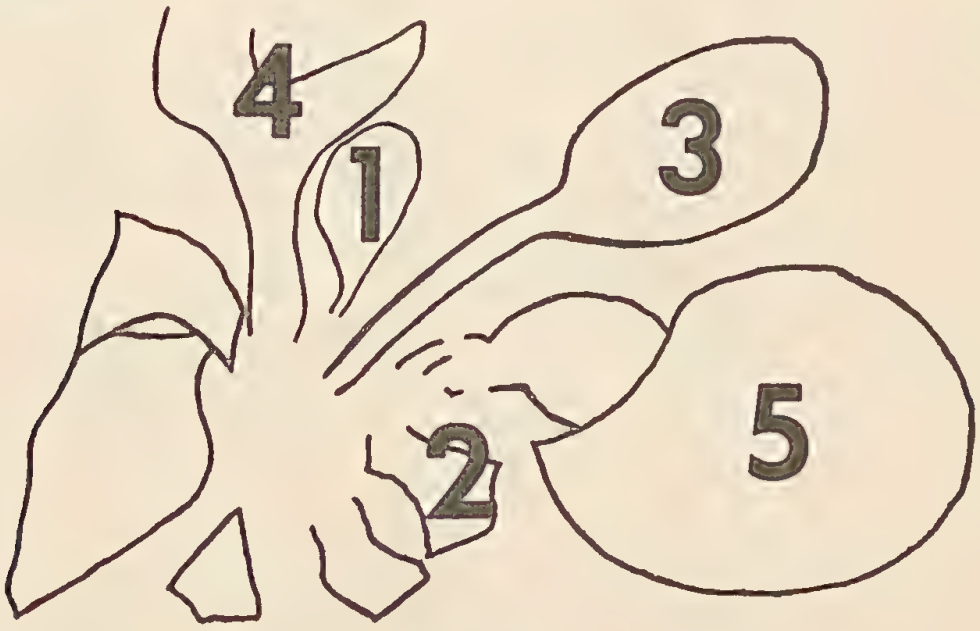
A single undifferentiated pit was obvious on most cushions. This was surrounded by a double row of small protuberances, 16 were counted on one cushion.

If abcission occurred after only a small number of leaves had expanded, then leaf fall would have occurred continuously throughout the growing season. It is possible that this specimen (i.e. the whole plant) was buried during the period of leaf fall. This may account for the tufted arrangement of leaves on shoots, but would not explain the number of young leaves present. I think that leaf fall must have continued throughout the growing season, although there might have been a time of the year when it was heavier.

The upper right hand spray on specimen F43529 (fig. 2) shows leaves arising at one per rib of the stem. This suggests that the ribbed stem is decorticated and represents a stele.

Leaf

It appears that leaves were at first erect, then after they expanded, they drooped. Text fig. 1 is a representation based on the tuft of leaves shown as fig. 17, and its counterpart, the lower left hand tuft of fig. 2. This will be used to illustrate leaf expansion.



Text Fig. 1

The series of leaves labelled 1 to 5 probably illustrates the normal mode of expansion. The term "leaf axis" is used to refer to the central portion of the leaf that would normally be occupied by a midrib, were one present.

The earliest stages of growth can only be postulated, that is from development in a primordium and initial expansion into a leaf. No evidence of this stage was found, such as a bud.

The size of the areoles formed by the secondary venation does not appear to differ markedly between the smallest and the largest of the leaves in the collection. Compare the areoles of the small leaves of specimens F43535 and F43587 (figs 6 and 11) with those of fully expanded leaves on the majority of figured specimens, e.g. F43562 (figs 4 and 5). The major difference between these two groups of leaves is that the smaller leaves appear to have a midrib, whereas the larger leaves have a series of stout parallel veins along the leaf axis.

The parallel central veins that form the leaf axis dichotomise, but do not anastomose. There are up to 7 of these veins across the width of a petiole. The divergent venation develops from the dichotomies of the axial venation. It is arched towards the margin. It dichotomises and anastomoses frequently. There is little or no decrease in width of areoles between the central and marginal portions of the leaf. The length of an areole may decrease by up to half over the same distance.

The following mode of expansion of the leaves is probable. Elongation of a primordial leaf into a thin, strap-like organ with an expanded head, possibly resembling a very small spoon. Lateral expansion of the strap-like organ into a leaf blade started near the expanded head, then extended downwards towards the attachment. The developing leaf continued to increase in length until approximately half of the total length of the leaf had expanded laterally. Thereafter, increase in length was slight, but lateral expansion continued downwards until only a short length of petiole remained. This was noticed in a number of tufts, but is illustrated best by the tuft shown as text fig. 1. As expansion continued, the tissue between the ribbing of the

midrib itself expanded so that the midrib dissolved into a series of strongly developed secondary veins that lay along the leaf axis. The *Glossopteris* juvenile leaf thus became a *Gangamopteris*.

The final stage in expansion appeared to be the development of a rhombic outline. This seemed to be most common in drooping leaves—leaves that no longer had the support of a coherent midrib. The lowermost leaf visible on fig. 16 is a leaf that was developing the rhombic outline. The leaves figured on the upper part of fig. 7, including the type specimen, its counterpart, fig. 5, and on figs. 1 and 4 have a well developed rhombic outline.

The leaf shown at the left of fig. 12 (specimen F43531) is unusual, it was the only oblong leaf found. In this specimen the leaves of the upper tuft had fallen, but the stem had not become decorticated as scars are visible between the upper and lower tufts.

TABLE 1

Dimensions in Millimetres of Leaves Designated in Text Fig. 1

	Leaf Number				
	1	2	3	4	5
Length of leaf	7	?	14	16	21
Width of half leaf	2.7	2.4	5.0	7.0	8.5
Length of petiole	5	4	11	6	5 est.
Width of petiole..	0.8	1.0	1.4	2.0	1.9
Veins per 2 mm at margin half way along leaf	9	7	9	7	6

Some organs described and illustrated occasionally in the literature probably represented juvenile leaves for the mode of expansion suggested, e.g. Johnston (1888) plate VIII, figs 10-14. Johnston described his specimens as "Impressions of young fronds resembling *Gangamopteris obliqua;* probably the rudimentary leaves of *Gangamopteris spatulata.*"

The resemblance of fig. 10 of Johnston to *Nephropsis tomiensis* Zalessky and his figs 13 and 14 to *Nephropsis elongata* Neuburg is striking. An observational difference between the above leaves and *Glossopteris* scale leaves on one hand and *Nephropsis* on the other, is also found in a comparison of *Glossopteris* and *Gangamopteris* with *Pursongia* and *Zamiopteris*. This is that the veins in anastomoses fuse in the Gondwana genera, but do not in the Angara genera.

Halle (1911) illustrated "an unusual form of *Gangamopteris*, or perhaps, rather a scale frond of a *Glossopteris*" (plate 8, fig. 10) that could be a juvenile leaf undergoing expansion into a normal *Gangamopteris* leaf. It appears to resemble *Nephropsis*. Many other scale leaves of *Glossopteris* resemble *Nephropsis cordata* Radczenko. This similarity between these *Nephropsis* species (a cordaitalean leaf) and juvenile or apparently juvenile forms of *Gangamopteris* and *Glossopteris* appears remarkable, particularly as some of the wood associated with occurrences of Lower Gondwana floras is of a cordaitalean type. This might tend to further support the idea of a parallel development of floras in Gondwanaland and Angaraland, as suggested by Neuburg (1954), rather than connection between the two areas.

The taeniopteroid leaf fragments shown on fig. 10 occurred commonly throughout the collection. As only fragments were seen, no attempt at identification was made.

Microstructures

Although many leaves had what appeared to be original coaly leaf material present, no cuticle could be recovered. Under reflected light very few leaves showed signs of microstructure (fig. 19).

Leaves of the lower whorl of specimen F43568 (fig. 13) and of specimen F43528 (fig. 17) showed cuticular structure of the upper epidermis. In both the cell pattern formed elongate-polygonal cells elongated along the direction of the venation. Cells along veins were more elongate than those between veins. Stomata appeared to be absent. Cell walls appeared to be straight.

Average dimensions of cells are 25-40μ long by 12-20μ wide along veins and 25-60μ long by 25-40μ wide between veins.

A number of specimens has tracheids visible within the veins. All such leaves appeared to be exposing the ventral surface. Specimen F43586 (leaf, top left of fig. 14, and enlarged in fig. 18) showed bundles of tracheids dividing and recombining with bundles of tracheids from adjacent veins at anastomoses. When tracheid bundles combined, the separate identity of the joining veins becomes completely lost. Tracheids appeared to be less than 10μ wide, and some in excess of 200μ long. Preservation precluded determination of the type of thickening present, or of the presence of pits. No cell structure was visible in interveinal regions.

Comparison

In a comparison with other species, it seems that *Gangampoteris walkomii* may be compared with other species of *Gangamopteris* in adult leaves only. For the comparison to be complete, the juvenile leaves must be compared with *Glossopteris* leaves. The habit must be considered separately too.

Adult leaves

The frequent anastomoses of the venation and the rhombic leaf shape separates *Gangamopteris walkomii* from all other species of *Gangamopteris*.

Juvenile leaves

The small ovate leaves have a venation pattern similar to that of *Gangampteris castellanosii* Archangelsky in disposition, but the Australian leaves are very much smaller, and have an apparent midrib. The leaves are similar in shape, and only slightly smaller than figured leaves of *Glossopteris orbicularis* White. In *Gangamopteris walkomii* the venation arches outwards similar to the arching of the secondary venation in *Glossopteris browniana*, but in *Glossopteris orbicularis* it arches upwards towards the apex.

Microstructure

Insufficient is known to give any valid separation from other species.

Habit

The leaves are arranged into tightly adpressed spirals. This seems to be characteristic of many *Glossopteris* and *Gangamopteris* species. Pant (1962) has recorded all previously reported attached specimens. The nature of the scars on the specimen described by Etheridge (1894) is very much broader compared with length than the scar in specimens of this collection. The specimen of Etheridge has deteriorated somewhat apprently because of dehydration, so only the scars shown by his pl. XVIII fig. 2 are still readily discernable. *Gangamopteris walkomii* has elliptical to rhombic leaves and lacks a midrib whereas the specimen of Etheridge (1894) along with others listed by Pant (1962) are lanceolate and have a midrib.

Plumstead (1959) discussed the habit of various glossopterids. Some of her postulates require review because of the evidence of habit shown by *Gangamopteris walkomii*. These are dealt with under the same headings as she used.

Evidence of habit from leaves

(a) Banks of fossilized leaves; and

(b) The evidence . . . concerning the mixed sizes of leaves.

Most clusters of leaves of *Gangamopteris walkomii* showed a mixture of leaves of different sizes growing together. Although leaves frequently were shed in clusters, these clusters were not broken during transport or burial under the prevailing conditions at Narrowneck. Plumstead suggested leaves might be shed in clusters and, during burial, the clusters broken or intermingled with many other clusters to form into matted bands. No bank of leaves occurred associated with this species, but it has been recognized only at this locality.

(c) New evidence of attached leaf clusters.

This is yet another species that had spirally arranged leaves that formed tufts or clusters.

(d) Suggested reasons for the paucity of evidence of *Glossopteris* in a position of growth.

Gangamopteris walkomii leaves and clusters were small enough to be readily recognizable in clusters on small slabs of rock, whereas most other glossopterid leaves were sufficiently big for clusters to be broken when the rock was split.

(e) Reconstruction of the leaf growth habit.

In common with other recorded clusters, leaves varied in size. This was to be expected when leaves expanded in succession along the shoot.

No fructifications were found associated with any of the leaves. There is no evidence where on a shoot the fructification may have developed, or whether it developed on a special fertile shoot.

Plumstead suggested that "clusters were normally shed as a whole, leaving probably a single large oval, or pear-shaped scar, and that in many cases the leaves remained together until they were buried." This is not so in *Gangamopteris walkomii* where leaves appeared to have been shed singly (figs 12 and 13). It would appear that were clusters shed as a whole, each cluster would represent a short shoot. In this species a terminal cluster would have to be shed, but not a short shoot, to give rise to fossil leaf clusters. The wood would have to be brittle and break at points of leaf growth, otherwise specimens such as shown on figs 1, 2, 6, 7, 8, 12, 13, and 16 would be common in many species. If the wood in this species had been sufficiently brittle to shed only terminal tufts, then preservation of specimens such as F43564 (fig. 8) would not be likely. It is possible that *Gangamopteris walkomii* had an unusually long short shoot. In other species tufts of leaves occur only in the form shown by *Gangamopteris walkomii* on fig. 9.

She then discussed the role of the scale leaf. There is no evidence here to suggest or favour any particular function of these organs, as scales were not found attached to shoots of *Gangamopteris walkomii*. She was apparently unaware of the shoots figured by Walkom (1928) showing scales attached in a position of growth (figs 1 and 2). From the spacing of the scales along the stem his shoots could not have been associated with vegetative shoots of *Gangamopteris walkomii*. His shoots bore *Nephropsis*-like scales.

The specimen of *Glossopteris* ? *angustifolia* shown as fig. 3 is from Thornley, N.S.W. These leaves are arranged in a tuft similar to *Gangamopteris walkomii* and the specimen figured by Etheridge (1894). He described his specimen as "undoubtedly comes near to *G. linearis*, McCoy, in a general habit of the leaves, and *G. Clarkei*, Feist., in the venation." It was found in the Permian outcrop near Cooyal (determined from Etheridge, 1904). Hence three species of glossopterid leaves were borne spirally on branches, besides the curious specimen described as *Glossopteris browniana* by Dana (1849; pl. 12, fig. 13c).

ACKNOWLEDGMENTS

Thanks are due to the former Director of the Australian Museum, Sydney, Dr. J. W. Evans, for permission to borrow and describe this collection; and to the former Deputy Director, Mr H. O. Fletcher, for arranging this permission, and for information concerning the locality and other pertinent matters. The examination was carried out in the laboratories of the Department of Geology, University of Newcastle, N.S.W.

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LEGEND

Gangamopteris walkomii sp. nov.

All specimens are held by the Australian Museum, Sydney, N.S.W. All figures are approximately natural size, unless otherwise noted.

PLATE 25

Fig. 1—Two shoots showing terminal groups of leaves. Specimen F43535.

Fig. 2—A number of groups of leaves showing how the closely adpressed phyllotaxy gives a verticillate appearance. The leaves have fallen from the branch in the upper right without leaving scars or cushions, but only a longitudinally striated stem. Specimen F43529 (obverse) (counterpart, enlarged, is shown as fig. 17).

Fig. 3—*Glossopteris* ? *angustifolia* Brongniart. Leaves showing probable similar arrangement to *Gangamopteris walkomii*. Specimen from unregistered collection 582, Mining Museum, Sydney, N.S.W. Enlarged x1¼.

Fig. 4—Leaves, some isolated. The uppermost leaf still shows a midrib although it has developed a rhombic shape. Specimen F43562 (reverse).

Fig. 5—Counterpart of the type specimen is shown on the left. Specimen F43562 (see also fig. 9) (counterpart to fig. 7).

Fig. 6—Juvenile leaves, broadly elliptical to almost circular, with a distinct midrib. Specimen F43535.

Fig. 7—Type specimen. The leaf vertically placed nearest to fig. 6 has been selected. Midrib has expanded into a series of coarse longitudinal veins. Other leaves of this specimen also show the longitudinal veins. Specimen F43563 (obverse) (counterpart to fig. 5).

Fig. 8—Paratype showing long and short shoots. The short shoot (lower centre) arose within a leaf axil of the long shoot. Leaves at the base of the short shoot droop backwards along the stem. Specimen F43564 (counterpart to fig. 16).

Fig. 9—Leaf cluster showing that leaves did not arise in a verticil, but in a closely adpressed spiral. Specimen F43562 (see also fig. 5).

PLATE 26

Fig. 10—Juvenile leaves and leaf fragments. The taeniopteroid fragments are common in the collection. Specimen F43584.

Fig. 11—Distorted juvenile leaves. The nature of the anastomosis of the secondary venation shows most clearly in the lowest leaf. Specimen F43587.

Fig. 12—Stem showing closely grouped, spirally arranged leaf cushions. The shape of the left hand leaf is unusual. Specimen F43531.

Fig. 13—Broadly expanded leaf bases are shown attached to the stem. The position of the abcission layer appears as a notch. Although these leaves are not small, they still appear to be stem clasping. The upper structure at right angles to the stem is a whorl that was damaged during splitting. Specimen F43568.

Fig. 14—Juvenile leaf fragments that have venation anastomosis of identical dimensions to that of adult leaves. Specimen F43586 (part of leaf at top left has been enlarged as fig. 18).

Fig. 15—Cross sections of stems. Specimen F43588 (reverse).

Fig. 16—Long and short shoots. The short shoot has been slightly bent below the lower leaf tuft. The stem of the short shoot is longitudinally ribbed. No leaf scars are visible. Specimen F43563 (reverse) (counterpart to paratype, fig. 7).

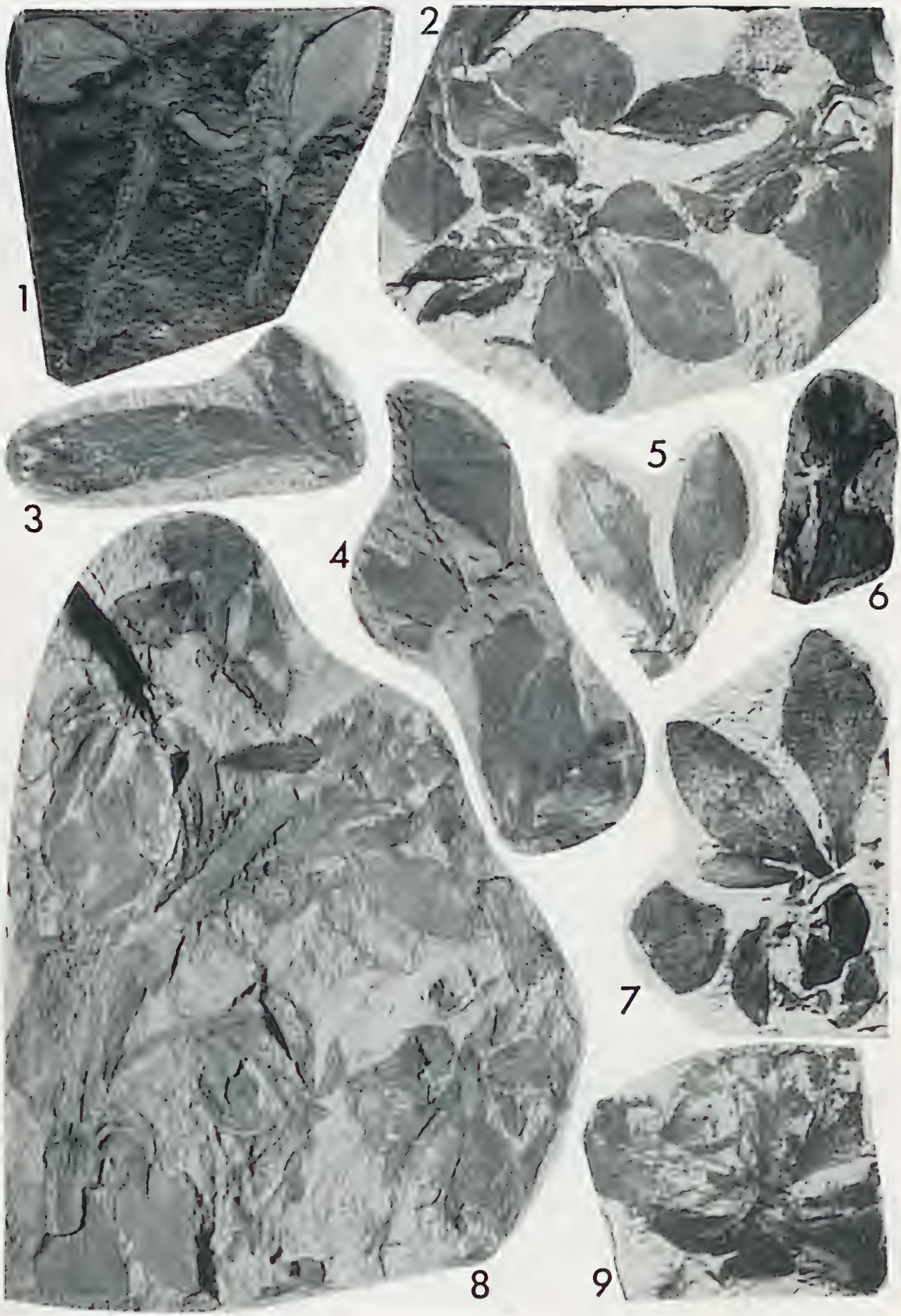
PLATE 27

Fig. 17—Tuft of leaves showing cushions left when leaves have fallen. Enlargement x 1¼ of specimen F43528 (counterpart to fig. 2).

Fig. 18—Leaf surface, assumed dorsal, enlarged to show tracheids of veins. Enlargement x 16 o specimen F43586 (leaf shown natural size as fig. 14).

Fig. 19—Ventral surface of leaf enlarged x 25 to show outline of cells. No stomata appear present. Specimen F43528.

Fig. 20—Stem fragment. Specimen F43529 (reverse).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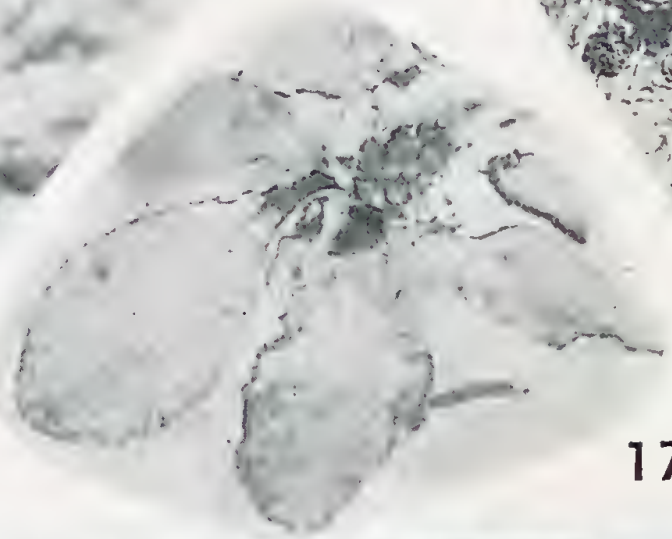

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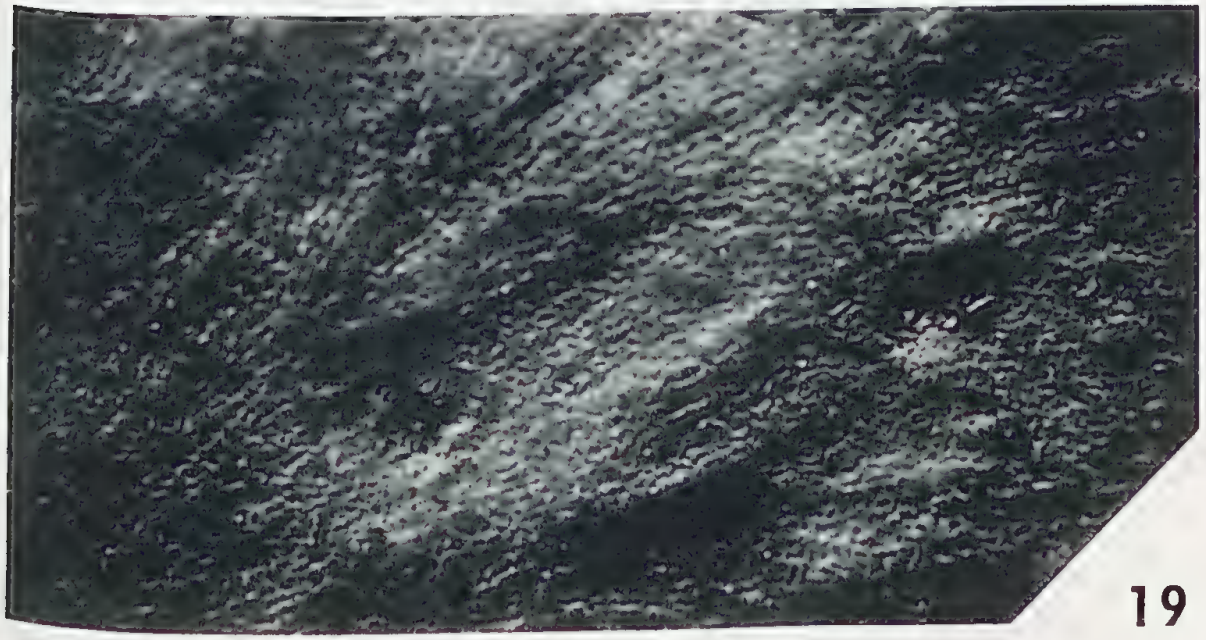

19

SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part 2: Metrical Features of *P. nasuta*

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Plates 28-31. Fig. 1. Manuscript received, 10th January, 1966.

This paper deals with an analysis of the sex and locality differences in the metrical features of the skull and teeth of the species *P. nasuta*. It is the second part of an overall study dealing with the variation in the skull and teeth of bandicoots of the marsupial genus *Perameles*. Part 1 (Freedman, 1967) included an anatomical description of the skull and teeth of *P. nasuta*, followed by a discussion of the anatomical variations in certain of these features in the different species of the genus.

MATERIALS AND METHODS

For the present study, a total of 111 specimens of *P. nasuta* were examined, 54 males and 57 females. The localities of these specimens were given in Part 1 and the material was described there as coming from 3 regions east of the Great Dividing Range (Queensland, New South Wales and Victoria) along the east coast of Australia. For the present analysis, the Queensland group was initially further subdivided into a northern and a southern sub-group. This was done partly to make 4 approximately equal geographical areas but also because the most northern Queensland specimens (from Ravenshoe, Cairns district) have been described (e.g., Iredale and Troughton, 1934) as representing a separate sub-species (*P. nasuta pallescens*). However, it can be seen from Table 1, in which the various groups studied are listed by sex and locality, that the numbers of specimens, especially of the females, are very small in the North and South Queensland groups. Because of this, after being used in the tests for the assessment of sexual dimorphism, these two groups had to be combined again for the multivariate analysis tests used to investigate possible locality differences.

A number of features of the skull and teeth were assessed non-metrically for use in the ageing and sexing of the material and also for the description of skull and tooth anatomy. These include: the degree of development of the temporal, sagittal and lambdoid crests; whether the posterior palatine vacuities were single or double; the presence and size of additional vacuities (i.e., additional to the usual anterior and posterior pairs); the degree of synostosis between (i) the 4 parts of the occipital bone, (ii) the 2 frontal bones and (iii) the basi-occipital and basi-sphenoid bones; and finally, the state of eruption and the amount of attrition of the teeth, especially of the canines, last premolar teeth and all of the molars. Relevant data on these features are given in various parts of the whole study.

Specimens in which the full dentition was not yet present (i.e. juvenile or "immature" specimens) were only used for measurements of those teeth which were fully erupted. No skull dimensions or tooth row measurements of these specimens were included in the main metrical studies. Specimens with all teeth fully erupted were termed "mature" and, on tooth wear (of the molars, mainly M3), were classed as young adult, adult or old adult. Although analysis of the point was not practical in the present study, it is clear from work by other authors (discussed in Part I) that some relatively small size increase does occur after the last tooth has fully erupted.

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Sexing (when not recorded) was done on the basis of canine structure and size. These differences are quite clear in *P. nasuta*, but become progressively less so in *Perameles gunnii* and the smaller species of the genus (see Part 1 and also Table 3 below).

The 27 skull and 50 tooth measurements used in this study were devised specifically for the project on the basis of those most commonly used in mammalian studies (e.g., Cockrum, 1957). Some additional measurements were added because of previous work (Kingsmill, 1962) and certain others because of the special anatomical features of the group. The 77 measurements used are defined in Appendix 1, which should be read in conjunction with Plates 28-31, which illustrate the main features of the skull and teeth of *P. nasuta*. As a number of the specimens used in the study were partially damaged, not all of the measurements could be taken on every specimen.

Most of the measurements were made with a dial caliper reading to 0.05 mm and readings were recorded to the nearest 0.1 mm. Certain awkward dimensions of the teeth were measured under a dissecting microscope with a calibrated eyepiece. The latter dimensions include: length of the last upper and lower premolars, buccal length of each upper molar and greatest length of each lower molar. These measurements were also recorded to the nearest 0.1 mm.

Because of the anatomical form of the various individual teeth, wear had to be considerable before its effects on the measurements taken were marked. Where this was the case, the relevant measurements were omitted. The effects of attrition were, as a rule, most marked on the molars, the upper teeth usually being affected before their lower equivalents and, in each, the length dimensions considerably before the breadths. Further, in the upper molars, the buccal length was affected before the lingual and, in the lower molars, the distal breadth before the mesial.

ANALYSIS

The skull and tooth data of *P. nasuta* were analysed to determine, firstly, whether sexual dimorphism was present and, secondly, whether groups of specimens from certain localities differed significantly in any particular measurements, or in the overall pattern of measurements.

(1) *Sex differences*

Sexual dimorphism in the metrical features of a species may take the form of differences between the male and the female variances, means, or both. Tables 2 (skull) and 3 (A-upper teeth, B-lower teeth) list the numbers of specimens, mean values and standard deviations for each of the 77 skull and tooth measurements of all of the males and of all of the females of *P. nasuta* studied. The standard deviations given in these Tables were found by regarding all of the males and all of the females as each forming a single, separate population.

For examining the metrical sex differences in *P. nasuta*, the male and female data were each treated as comprising separate samples from 4 localities (North Queensland, South Queensland, New South Wales and Victoria) in view of possible locality differences. For each measurement estimates of the overall male and the overall female variances were obtained by pooling the estimates from each of the 4 localities. When these pooled male and female variances were compared by an F test, significant results were obtained at the 1 per cent level in a considerable number of instances, but mainly in the skull measurements (Tables 2 and 3). Thus, in the skull, males and females of *P. nasuta* differ in their variances in 14/27 measurements at the 1 per cent level and in another 3 measurements at the 5 per cent level; in the teeth, the two sexes differ in 8/50 at the 1 per cent level and in a further 3 measurements at the 5 per cent level.

Examination of the differences between the variances of the 8 populations showed that, particularly in the case of the skull measurements, they were not in general proportional to the differences between the equivalent mean values. A simple

transformation for stabilizing the variances was thus not available. Because of this (and the significant F test findings), the "t" test was not applicable for comparing the mean values of males and females of this species. The standard Aspin-Welch test (Pearson and Hartley, 1954) was thus modified to take account of the fact that each of the two means (male and female) was itself the average of 4 means based on varying numbers of observations. By this test, significant results were found at the 2 per cent level in 23/27 skull measurements and in 40/50 of the tooth measurements; at the 10 per cent level, a further 1 measurement was significant in the skull and 4 in the teeth. Males and females thus differ considerably in their mean values for measurements of both the skull and the teeth. Further, inspection of Tables 2 and 3 shows that in all 77 measurements, the male mean figure is greater than that for the female.

(2) *Locality differences*

The significant sex differences found clearly indicated that separate analysis of the two sexes was necessary for the study of possible locality differences. An examination of the data for the 4 male and the 4 female populations showed that the locality differences are not as marked as the sex differences. This can be seen in Tables 4 and 5 which include the mean values for 10 skull and 10 dental dimensions for males and females separately from the 4 localities. It was consequently apparent that some form of multivariate analysis was necessary in order to compare material of *P. nasuta* from different localities.

Ten dimensions were selected from the skull measurements and 10 from the dental measurements (Tables 4 and 5). These particular dimensions were chosen (a) for their representation of different parts and different types of measurements of the skull and teeth, (b) because inspection of the full table of basic data suggested that certain features might be of particular interest with regard to their distribution over the 4 localities and (c) for the technical requirement of obtaining completeness of data on a maximum number of specimens.

Using 4 localities, the numbers of specimens in each of the 8 populations which included either all of the 10 skull measurements or all of the 10 dental dimensions, were clearly too small to make comparisons meaningful. For the first set of multivariate tests, it was therefore decided to re-arrange the relevant material of each sex into 2 groups to obtain reasonable numbers of specimens for each comparison. North and South Queensland were added together to form a northern group and New South Wales and Victoria were combined to make a southern group. For each sex, the resulting 2 populations were then compared separately for the 10 skull and the 10 tooth measurements by Mahalanobis' D^2 (Rao, 1952). The results of the tests are listed in Table 6 and were all found to be significant at the 1 per cent level. The differences indicated by the D^2 values are greater in the males than in the females and, within each sex, are greater in the skull features than in those of the teeth.

As the above D^2 values were so clearly significant, the data were re-arranged into 3 groups (Queensland (Q)—in the north, New South Wales (N.S.W.)—central and Victoria (V)—in the south) and, using the same 2 sets of characters, the various D^2 values were calculated. The results of this examination (Table 7 and Fig. 1) are far less clear than those using 2 localities. From the female comparison, in both the skull and the teeth, it appears that there is a greater difference between N.S.W. and V than between Q and N.S.W.; the difference between Q and V is clearly the greatest in both cases. In the male comparison, in both the skull and the teeth, N.S.W. and V differ by less than Q and N.S.W.; in the teeth the Q and V comparison is only just the largest, whilst in the skull, the Q and V figure lies between those of the other two tests. Because of the small numbers involved, significance tests were not applied to these results.

Because of the nature of the foregoing results, there seemed little point in attempting a 4 locality multivariate comparison. Instead, as the question of a possible north-south clinal change in size was of interest, and inspection of the relevant data suggested that the northern specimens were very frequently larger than the southern, especially in the skull (e.g. Tables 4 and 5), an attempt was made to assess the size difference between the northern and southern specimens.

For this test, males and females of the north-south population subdivision were used and 3 measurements were selected (maximum length, cranial breadth and occipital height) which could be considered as illustrating overall cranial size. Standardized mean values were subtracted (north minus south) for each of the 3 characters in males and females separately and the sum of the differences was found to be positive for each sex. These sums of differences are proportional to the square roots of the size measurement (C^2Q) of Penrose (1954). On being tested for significance by an appropriate "t" test which allows for intercorrelations, the male figure ($t = 2.16$, with 26 d.f.) was found to be significant at the 5 per cent level; the female figure ($t = 1.28$, with 28 d.f.) was not significant.

DISCUSSION

The F and Aspin Welch tests have clearly shown the degree of sexual dimorphism in the species *P. nasuta*. In their variances, the significant metrical differences are mainly restricted to certain of the measurements of the skull, tooth rows and canine teeth, but in their mean values, males were found to be significantly larger than females in almost all of the measurements of both the skull and teeth (Tables 2 and 3).

The D^2 comparisons between the northern and southern subdivisions of the species, revealed a clear, significant difference between the selected skull and tooth measurements in both the males and females. Differences are greater in the males than in the females and more marked in the skull measurements than in those of the teeth.

In the 3 population multivariate analysis, the D^2 values obtained did not suggest as clear cut inter-relationships (Fig. 1). Of the 3 populations, geographically the most northerly is Queensland (Q) and the most southerly Victoria (V), with New South Wales (N.S.W.) lying between the two. In the females, the Q-V value is greater than that of either of the other 2 comparisons in both the skull and the teeth and further, the N.S.W.-V values are greater than the Q-N.S.W. values in both cases. In the males, however, the Q-V value is slightly greater than either of the other 2 values in the tooth comparison, but in the skull comparison, it is less than the Q-N.S.W. value. Also, in this sex the Q-N.S.W. value is considerably greater than the N.S.W.-V value in both the skull and the tooth comparisons, which is the opposite of what was found in the females. Thus no general meaningful clinal pattern appears to emerge from the 3 population comparisons—quite possibly because of the small numbers of specimens available, particularly from Victoria (V). Because of these results and the similarily small numbers of specimens available from North Queensland, it was felt that the possibility of a metrical difference in that region did not merit further investigation on the present data.

In the comparison of overall cranial size between north and south based on 3 characters, it was found that the northern males and females were larger than their southern counterparts, but only in the case of the males was the difference found to be significant at the 5 per cent level. Although the observed female difference was less than the corresponding male figure, it is felt that this female difference is real and that the non-significant result obtained could have arisen from the relatively small numbers of specimens involved, particularly in the northern group (7). If this is so, it is of interest to note than an increase in size for *P. nasuta* from the cooler south to the subtropical north runs contrary to "Bergmann's Rule", which states that, within a

warm-blooded vertebrate species, there should be a size decrease in a warmer climate. A number of exceptions to the "rule" have, however, been recorded (Rensch, 1959: pg. 43).

Examination of the full data for the 27 skull measurements for the north-south subdivision of the species supports an hypothesis that, in most instances skull dimensions are larger in the north than in the south in both sexes. However, study of equivalent data for the 50 tooth measurements, seems to indicate that, in both males and females, these measurements vary randomly with respect to whether the northern or the southern mean values are larger.

It therefore seems reasonable to conclude that the significant difference found for the 10 skull character comparison between northern and southern males of *P. nasuta* depends, at least in part, on a south to north size increase. It is felt that there is a similar size increase in the female skull measurements, but this has not been established conclusively. On the other hand, in the corresponding tooth comparisons, the significant differences found between north and south in both the males and the females would not appear to be attributable to a size increase in either direction.

SUMMARY

(1) The metrical features of the skulls and teeth of 111 specimens of *P. nasuta* from various localities on the east coast of Australia have been studied.

(2) In their mean values, males were found to be significantly larger than females for most of the 27 skull and 50 tooth measurements analysed, but, in their variances, the 2 sexes only differed in certain of the skull, tooth row and canine teeth dimensions.

(3) In a north-south subdivision of the species, significant differences were found, in both males and females, by multivariate analysis of selected groups of skull and tooth measurements. In a 3-fold subdivision of the species, no clinal pattern was apparent.

(4) The significant north-south difference in the skull measurements is, at least in the case of the males, partially the result of a size increase from south to north. The corresponding significant differences in the tooth measurements of both sexes do not appear to be attributable to a systematic, regional size increase.

ACKNOWLEDGMENTS

The computations for this study were carried out on the I.B.M. 1620 of the Duchess Computing Laboratory at the University of New South Wales.

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APPENDIX 1: MEASUREMENTS OF THE SKULL AND TEETH (PLATES 28-31)

In general, all of the measurements are maxima—length measurements being antero-posterior, breadths bilateral and heights dorso-ventral—but modified by the points and planes given in the various definitions. Where measurements are unilateral the left side was used, unless it was damaged. The special terms used below to facilitate the description of the measurements are modified from anthropological usage (Martin and Saller, 1957).

Cranium

(a) Length—

Maximum (Max.): Most anterior point on premaxillae (prosthion) to most posterior point of cranium (on lambdoid crest or occipital bone).

Basal (Bas.): Prosthion to most anterior point on foramen magnum (basion).

Condylo-basal (Cond.-Bas.): Prosthion to most posterior part of condyles.

Palatal (Pal.): Prosthion to most anterior point of posterior border of palate (on palatine bone).

Nasal (Nas.): Most anterior point on nasal bones to naso-frontal suture in dorsal midline (nasion).

Frontal (Fr.): Nasion to fronto-parietal suture in midline (bregma).

Parietal (Par.): Bregma to parieto-occipital suture in midline (lambda).

Premaxilla anterior to I^1 (Ant. to I^1): Prosthion to most posterior point on I^1 alveolus. (Taken to enable basal and palatal to be converted to basilar and palatar).

(b) Breadth—

Muzzle anterior to C (Ant. to C): Between sides of muzzle, just anterior to C teeth.

Muzzle at M^2 (At M^2): Between the external alveolar margins of maxillae, at midpoints of M^2 teeth.

Interorbital (Int.-Orb.): Between the lacrimal margins of the orbits, just above the malar bones.

Minimum frontal (Min. Fr.): Minimum post-orbital constriction of cranial roof, on frontal bones.

Bizygomatic (Bizyg.): Between most lateral parts of outer surfaces of zygomatic arches.

Cranial (Cran.): At base of cranium, on subsquamosal foramina i.e. just posterior to zygomatic arches and anterior to lambdoid crests.

(c) Height—

Anterior to C (Ant. to C): Alveolar margin anterior to C (below) to internasal suture (above), at right angles to dorsal muzzle profile.

Posterior to M^4 (Post. to M^4): Alveolar margin posterior to M^4 (below) to interfrontal suture (above), at right angles to dorsal muzzle profile.

Cranial (Cran.): Basion to bregma.

Occipital (Occip.): Basion to lambda (on occipital, above).

(d) Alisphenoid bulla (bulla)—

Length (L): Length axis runs anteromedially from external auditory meatus. (Measurement does not include otic bone).

Breadth (B): At right angles to length axis.

(e) Palatal vacuities (vacuities)—

Anterior palatal vacuity length (A.P.Vac.L.): Anteroposterior measurement of the longer of the pair.

Posterior palatal vacuity length (P.P.Vac.L.): As A.P.Vac.L.

Posterior palatal vacuity breadth (P.P.Vac.B.): Between lateral margins of the two vacuities.

Mandible

Maximum length (Max. L.): Most posterior part of one condyle to most anterior point of same half of mandible.

Length of Ramus (Ramus L.): Between the anterior and posterior borders of the ramus, from midpoint of posterior border and at right angles to ramus midline.

Breadth at M_2 (Br. at M_2): Thickness of body below M_2.

Height at M_2 (Ht. at M_2): Alveolar margin at middle of M_2 (above) to inferior border of mandible (below), at right angles to the alveolar margin.

Teeth

(a) Rows—

I1–M4—

Upper: More anterior labial surface of I^1 to distal surfaces of both M^4 teeth, all at level of alveolar margin.

Lower: Mesiolabial part of incisal tip of I_1 to distal surface of M_4 at alveolar margin.

Incisors—

Upper: Along incisal edge, from most mesiolabial point of I^1 to most distal point of I^4.

Lower: Along incisal edge, from most mesiolabial point of I_1 to most distal point of I_3.

C–M4—

Mesial surface of C to distal surface of M4, both at level of alveolar margin.

M–1M4—

Most mesial part of M1 to most distal part of M4, both on enamel-covered crown.

(b) Canines—

Length (L): Mesiodistal measurement at alveolar margin.

Breadth (B): Labiolingual measurement at alveolar margin.

Height (H): Mesial edge at alveolar margin to incisal tip.

(c) Premolars—

Length (L)—

P1 and P2: Maximum mesiodistal measurement on enamel-covered crown.

P3: Most mesial point of tooth at alveolar margin to most distal point.

Breadth (B)—

Maximum buccolingual.

(d) Molars (All taken on enamel-covered crown)—

Upper—

Breadth (B): Maximum buccolingual.

Length, buccal (LB): Maximum mesiodistal on buccal half of tooth.

Length, lingual (LL): Maximum mesiodistal on lingual half of tooth.

Lower—

Breadth, mesial (BM): Maximum buccolingual of mesial triangle.

Breadth, distal (BD): Maximum buccolingual of distal triangle.

Length (L): Maximum mesiodistal.

Table 1

Numbers of specimens of *P. nasuta* studied, listed by sex and locality

	Males	Females	Total
N.Q.	8	5	13
S.Q.	12	4	16
N.S.W.	19	35	54
VICT.	15	13	28
TOTAL	54	57	111

Table 2

Comparison of *P. nasuta* male and female skull measurements (in mm)

Measurement	Males			Females			F Test	A-W Test
	N	$\bar{X}$	SD	N	$\bar{X}$	SD		
Cranium—								
(a) length—								
Max.	32	88.80	6.26	32	80.61	3.10	**	**
Bas.	30	80.97	5.34	30	73.12	2.80	**	**
Cond.-Bas.	32	85.02	5.64	30	77.17	2.78	**	**
Pal.	31	54.29	3.04	31	50.03	1.60	**	**
Nas.	34	39.68	2.45	30	36.00	1.56	*	**
Fr.	37	27.02	2.03	34	24.85	1.41	ns	**
Par.	36	16.08	1.84	34	14.53	1.00	**	**
Ant. to I^1	30	3.22	0.31	30	3.00	0.22	ns	**
(b) breadth—								
Ant. to C	34	9.17	0.70	34	8.03	0.50	ns	**
At M^2	36	21.21	1.13	33	19.36	0.79	*	**
Int.-Orb.	35	25.47	1.19	32	23.76	1.02	ns	**
Min. Fr.	37	14.17	0.45	34	13.90	0.49	ns	*
Bizyg.	32	34.79	2.36	30	30.97	1.22	**	**
Cran.	34	25.48	1.64	32	23.40	0.95	**	**
(c) height—								
Ant. to C	32	7.31	0.59	32	6.31	0.40	*	**
Post. to M^4 ..	36	18.58	0.73	32	17.30	0.54	ns	**
Cran.	33	25.46	1.58	32	23.33	0.94	**	**
Occip.	33	19.87	1.56	32	17.93	0.83	**	**
(d) bulla—								
L	34	5.39	0.60	30	4.98	0.30	**	**
B	34	6.03	0.30	31	5.99	0.21	ns	ns
(e) vacuities—								
A.P. Vac. L. ..	32	9.19	0.87	32	8.25	0.46	**	**
P.P. Vac. L. ..	34	8.30	1.03	31	7.88	0.97	ns	ns
P.P. Vac. Br. ..	35	9.02	2.06	30	8.44	0.69	**	ns
Mandible—								
Max. L.	35	68.41	4.25	34	62.59	2.36	**	**
Ramus L.	35	9.53	0.98	34	8.03	0.73	ns	**
Br. at M_2	36	3.84	0.46	35	3.23	0.28	**	**
Ht. at M_2	36	7.23	0.75	35	6.15	0.70	ns	**

Significance level:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 3A

Comparison of *P. nasuta* male and female upper tooth measurements (in mm)

Measurement	Males			Females			F Test	A-W Test
	N	$\bar{X}$	SD	N	$\bar{X}$	SD		
I^1 — M^4	32	48.19	2.34	31	44.43	1.02	**	**
I^1 — I^4	39	5.97	0.26	42	5.87	0.32	ns	ns
C — M^4	35	34.29	1.65	33	31.39	0.66	**	**
M^1 — M^4	41	15.08	0.54	42	14.54	0.52	ns	**
C L	32	4.19	0.58	33	2.32	0.28	**	**
B	32	2.07	0.37	34	1.09	0.08	ns	**
H	31	6.28	1.49	32	3.24	0.41	ns	**
P^1 L	47	2.87	0.15	53	2.78	0.12	ns	**
B	53	1.13	0.07	55	1.06	0.07	ns	**
P^2 L	50	2.89	0.11	54	2.82	0.14	ns	**
B	51	1.50	0.10	55	1.45	0.12	ns	*
P^3 L	32	3.98	0.37	33	3.52	0.28	ns	**
B	40	2.18	0.17	41	2.03	0.18	ns	**
M^1 B	50	3.06	0.13	53	2.94	0.10	ns	**
LB	43	4.26	0.16	52	4.12	0.15	ns	**
LL	47	2.86	0.21	53	2.79	0.17	ns	ns
M^2 B	48	3.40	0.16	55	3.29	0.12	ns	**
LB	45	4.20	0.13	53	4.10	0.16	*	**
LL	48	2.82	0.17	54	2.76	0.15	ns	*
M^3 B	44	3.85	0.17	45	3.75	0.13	ns	**
LB	46	4.47	0.17	44	4.42	0.15	ns	**
LL	44	2.65	0.13	44	2.63	0.15	ns	ns
M^4 B	41	2.71	0.20	40	2.70	0.24	ns	ns
LB	39	3.77	0.21	42	3.50	0.32	ns	**
LL	41	1.54	0.14	41	1.52	0.14	ns	ns

Significance levels:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 3B

Comparison of *P. nasuta* male and female lower tooth measurements (in mm)

Measurement	Males			Females			F Test	A-W Test
	N	$\bar{X}$	SD	N	$\bar{X}$	SD		
I_1 — M_4	30	46.55	1.75	30	43.16	0.89	**	**
I_1 — I_3	46	4.94	0.30	46	4.84	0.25	ns	ns
$\overline{C}$ — M_4	33	36.73	1.85	34	33.39	0.78	**	**
M_1 — M_4	41	16.02	0.52	42	15.52	0.58	ns	**
$\overline{C}$ L	31	4.11	0.68	35	2.42	0.29	**	**
B	31	1.77	0.33	35	0.98	0.06	**	**
H	31	4.27	0.93	35	2.60	0.31	**	**
P_1 L	49	2.93	0.13	51	2.80	0.13	ns	**
B	52	1.03	0.06	53	0.96	0.06	ns	**
P_2 L	47	3.29	0.13	54	3.20	0.13	ns	**
B	52	1.30	0.08	55	1.24	0.09	ns	**
P_3 L	35	4.10	0.37	36	3.66	0.34	ns	**
B	40	1.52	0.12	42	1.42	0.10	ns	**
M_1 BM	49	2.03	0.09	53	1.96	0.07	ns	**
BD	46	2.43	0.12	53	2.31	0.09	ns	**
L	45	3.54	0.17	50	3.46	0.16	ns	*
M_2 BM	51	2.35	0.09	54	2.29	0.09	ns	**
BD	49	2.63	0.13	54	2.55	0.09	*	**
L	47	4.12	0.13	51	3.99	0.19	ns	**
M_3 BM	51	2.48	0.08	54	2.42	0.08	ns	**
BD	49	2.58	0.14	51	2.47	0.11	ns	**
L	47	4.30	0.14	53	4.17	0.17	ns	**
M_4 BM	46	2.38	0.11	45	2.35	0.10	ns	*
BD	41	1.63	0.13	45	1.58	0.13	ns	**
L	41	4.72	0.30	44	4.57	0.23	*	**

Significance levels:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 4

Mean values (in mm) of 10 selected skull measurements in 4 populations of *P. nasuta*

Measurement	Males				Females			
	N.Q. N = 6	S.Q. N = 6	N.S.W. N = 10	Vict. N = 6	N.Q. N = 3	S.Q. N = 4	N.S.W. N = 19	Vict. N = 4
Max. L.	90.97	92.90	86.05	88.72	79.57	82.90	80.19	79.85
Pal. L.	55.28	55.90	53.12	54.55	49.70	51.02	49.88	49.90
Fr. L.	28.00	28.90	25.74	27.02	25.07	25.85	24.41	25.88
Min. Fr. Br. ..	14.03	13.80	14.23	14.52	13.23	14.15	13.92	14.18
Cran. Br. ..	25.53	26.85	25.32	25.40	23.43	24.25	23.29	23.10
Mand. Ram. L. ..	10.00	10.37	9.36	9.22	8.17	8.35	8.06	7.25
Occip. Ht. ..	19.97	21.53	19.15	19.78	17.73	18.55	17.99	17.58
Mand. Ht. ..	7.85	7.93	6.74	7.22	6.13	6.70	6.05	5.75
P.P. Vac. L. ..	8.62	8.62	8.06	7.77	8.60	8.00	8.04	6.88
P.P. Vac. Br. ..	10.27	10.02	8.90	8.82	9.00	9.02	8.18	8.50

Table 5

Mean values (in mm) of 10 selected tooth measurements in 4 populations of *P. nasuta*

Measurement	Males				Females			
	N.Q. N = 4	S.Q. N = 7	N.S.W. N = 13	Vict. N = 9	N.Q. N = 4	S.Q. N = 4	N.S.W. N = 25	Vict. N = 5
P^1 L	3.00	2.94	2.88	2.84	2.92	2.75	2.81	2.70
P^2 B	1.58	1.57	1.49	1.46	1.65	1.45	1.49	1.34
M^1 LL	2.68	3.04	2.97	2.73	2.90	2.78	2.83	2.56
M^2 LL	2.75	2.96	2.93	2.73	2.82	2.82	2.83	2.58
M^3 B	3.95	3.94	3.80	3.77	3.70	3.78	3.78	3.60
P_1 L	3.08	2.96	2.89	2.79	2.90	2.75	2.81	2.76
M_1 BM	2.08	2.06	2.02	2.00	2.05	1.95	1.97	1.96
M_1 BD	2.42	2.50	2.43	2.42	2.38	2.35	2.32	2.24
M_4 BM	2.35	2.31	2.42	2.48	2.30	2.25	2.36	2.36
M_4 L	4.62	4.54	4.89	4.80	4.62	4.32	4.63	4.44

Table 6

D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 2 population subdivisions (north, Queensland; south, New South Wales and Victoria)

	Skull	Teeth
Males	14.9**	9.5**
Females	9.3**	6.5**

** Significant at 1% level.

Table 7

D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 3 population subdivisions

SKULL

	Males		
	Q.	N.S.W.	Vict.
Q. ..		20.2	13.7
N.S.W. ..	8.8		9.6
Vict. ..	24.2	16.1	
Females			

TEETH

	Males		
	Q.	N.S.W.	Vict.
Q. ..		11.2	12.1
N.S.W. ..	6.4		5.0
Vict. ..	35.1	19.9	
Females			

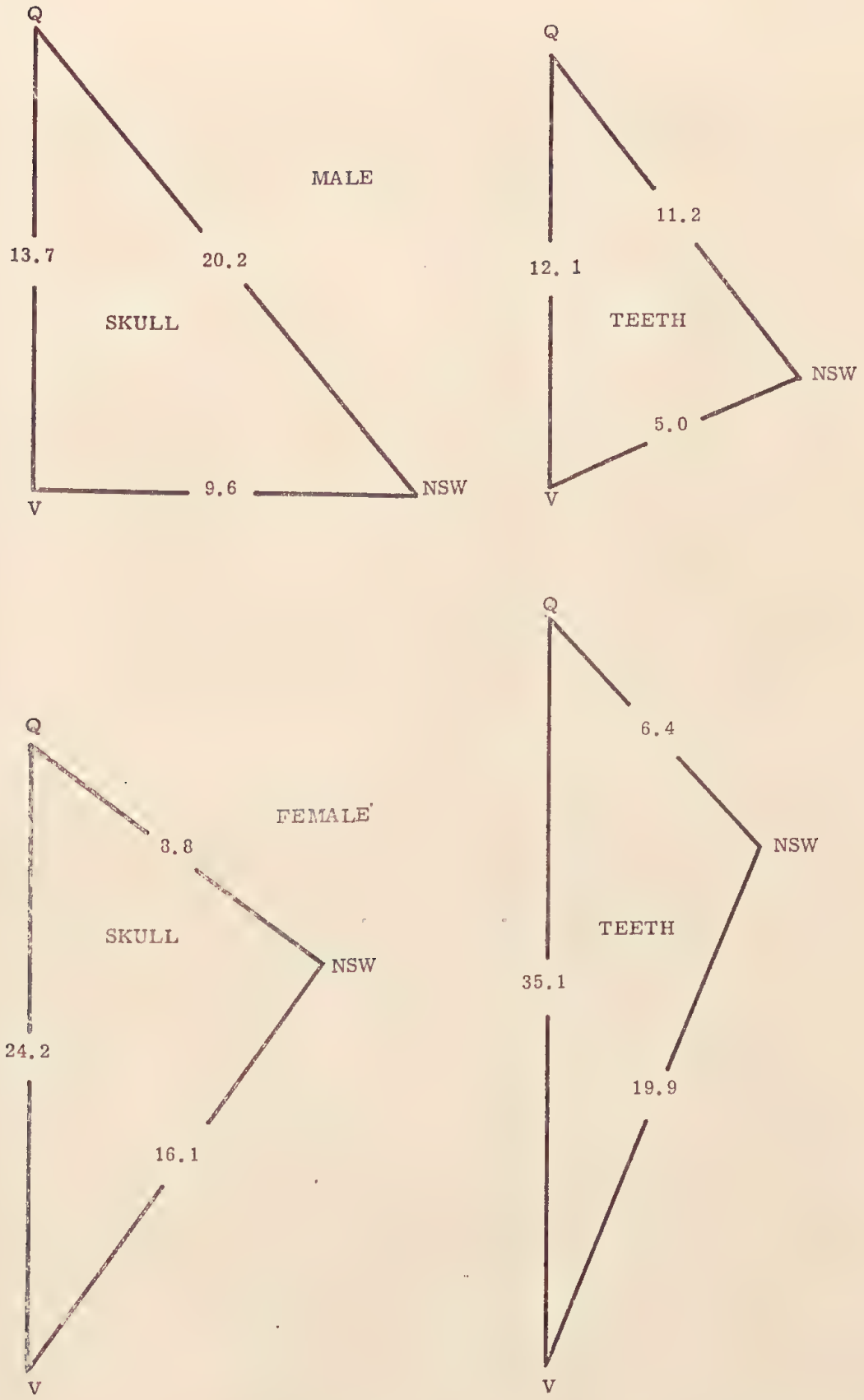
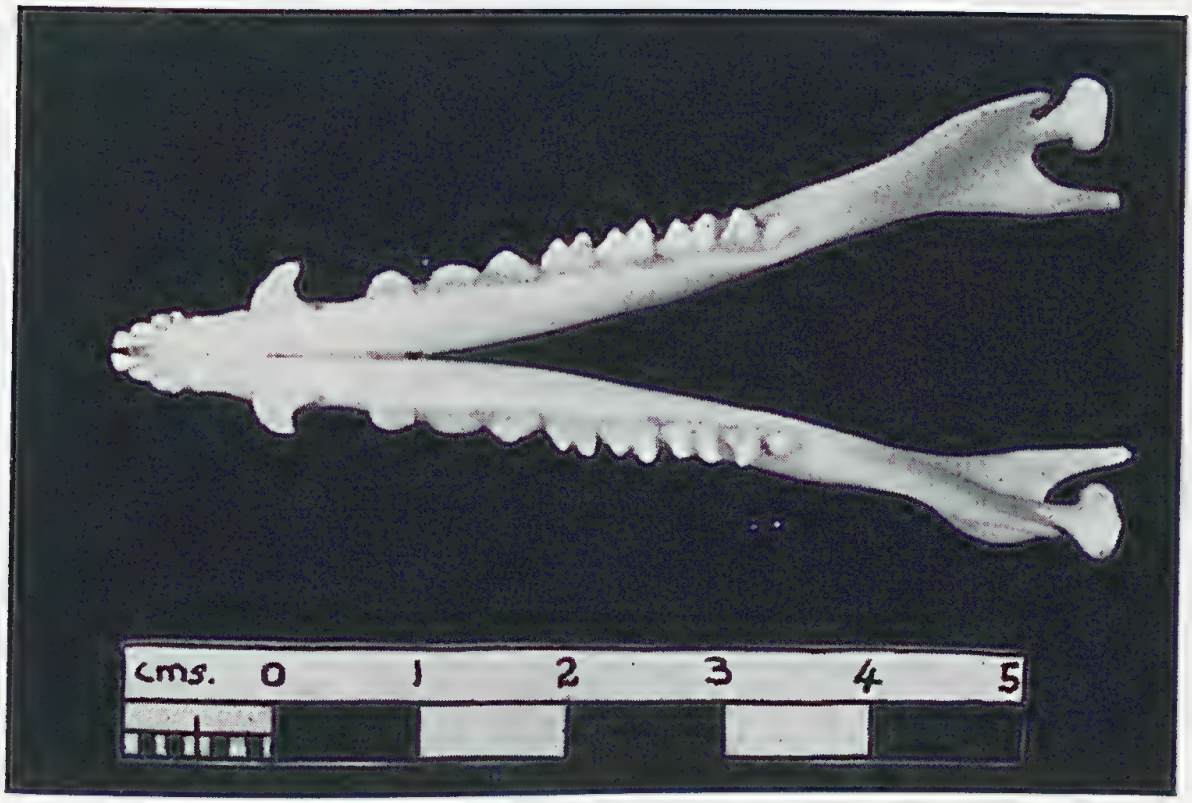


Fig. 1—Diagrams based on D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 3 population subdivisions. (Distances plotted are D values).

Plate 28 (above).—*P. nasuta*, male (M.8231). Cranium: norma dorsalis.
Plate 29 (below).—*P. nasuta*, male (M.8231). Cranium: norma basalis.

P. nasuta, male (M.8231) and female (M.8310). Skull: norma lateralis.



P. nasuta, male (M.8231). Occlusal view of mandible.

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SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part 3: Metrical Features of *P. gunnii* and *P. bougainville*

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Plates 32-34.

Manuscript received, 10th January, 1966.

This paper is concerned with the intraspecific variation of the metrical features of the skull and teeth in the long-nosed bandicoot species *Perameles gunnii* and *Perameles bougainville*. Part 1 of the study (Freedman, 1967) listed the numbers of specimens and the source and localities of the material used and reviewed the taxonomy of the genus. A description of the anatomy of the skull and teeth of *P. nasuta* was also given and some of the anatomical differences found in *P. gunnii* and *P. bougainville* were discussed. Part 2 (Freedman and Joffe, 1967) described the system of measurements and ageing and sexing criteria used in the study and analysed the sex and locality variations in the metrical features of the skull and teeth of *Perameles nasuta*.

MATERIALS AND METHODS

Of the species *P. gunnii*, 51 specimens were available for study: 14 males and 9 females from south-western Victoria (possibly overlapping into south-eastern South Australia) and 12 males and 16 females from various parts of Tasmania. The *P. bougainville* material (43 specimens) consisted of: (i) *P. bougainville notina*—13 specimens from south-western South Australia and 4 from the adjacent south-eastern Western Australia, (ii) *P. bougainville bougainville*—5 specimens from Dorre and Bernier Islands in Shark Bay off the central part of the west coast of Western Australia, and (iii) 5 specimens widely scattered through the central western part of the continent, some or all of which come from an area in which *Perameles eremiana* is said to occur. In addition there was a group of 16 specimens (4 adult and 12 immature or juvenile) for which no localities were available, but which metrically and anatomically seemed clearly to belong in the *P. bougainville notina* group. The above material was all described more fully in Part 1 and the localities of the various specimens were plotted on a map. The definitions of the measurements taken, criteria for sex and age and other aspects of methods and technique were discussed in detail in Part 2.

ANALYSIS

1. *P. gunnii* (plate 32).

(a) Metrical characteristics and sexual dimorphism.

In Tables 1 and 2 the numbers of specimens used and the mean values and standard deviations of the 77 skull and tooth measurements of the males and females of the pooled *P. gunnii* specimens from Victoria and Tasmania are tabulated. In addition, the results of F tests, for comparison of the variances of the 2 sexes, and Aspin-Welch tests (Pearson and Hartley, 1954), for comparing the male and female mean values, are listed.

The comparisons of the male and female variances of the skull measurements have yielded significant F test values at the 1 per cent level, in the nasal length and maximum length and height at M_2 of the mandible; in the teeth, the measurements significant at this level are, $\underline{C}$—M^4, M^3 labial length, $\overline{C}$—M_4 and $\overline{C}$ length. At the 5 per cent level, maximum, basal, condylo-basal, and anterior to I^1 lengths, bizygomatic breadth and cranial height are significant in the skull; whilst in the tooth measurements I^1—M^4, $\underline{C}$ height, I_1—M_4 and M_4 distal breadth are significant. Because of these results and the fact that, in general, the differences between the variances were not proportional to the equivalent differences between the mean values, the Aspin-Welch test was employed instead of the t-test for comparing the mean values of the 2 sexes.

Examination of the male and female mean values for the skull measurements shows that, except for the breadth measurements of the cranium, the male mean values are larger than those of the females in almost every case (19/21) and in the remaining 2 they are equal. In the breadth measurements the females are larger in 4/6 measurements. However, when these differences are examined by Aspin-Welch tests, only the maximum length of the mandible is significant at the 2 per cent level and the palatal and nasal lengths and the alisphenoid bulla breadth at the 10 per cent level.

In the tooth measurements, the mean values for the canine teeth measurements of the 2 sexes are all significantly different by Aspin-Welch tests at the 2 per cent level; the male mean value being larger in each case. In the tooth row measurements, Aspin-Welch tests of the mean values for the 2 sexes of $\underline{C}$—M^4, I_1—M_4 and $\overline{C}$—M_4 are significantly different at the 2 per cent level and I^1—M^4 and I^1—I^4 are significantly different at the 10 per cent level, the male mean value being larger in each case. In the remaining tooth measurements, the male or female measurement is equally frequently larger (male larger in 17/36 and 2 equal to female). Amongst these remaining tooth measurements, the breadths of P^1, P^2, M^1 and M^2 differ significantly by Aspin-Welch tests at the 2 per cent level and M^4 buccal length, P_2 breadth, and P_3 breadth and M_2 length are significantly different at the 10 per cent level, the male mean being the larger in all except 2 instances (M^1 and M^2 breadths).

(b) Locality differences.

Because of the significant differences found in the sexual dimorphism analysis, males and females were compared separately to determine whether there were significant differences between the Victorian and Tasmanian samples of the species.

Examination of the mean values for the 27 skull measurements for the 2 localities showed that there appeared to be a size difference between the 2 populations. The Tasmanian sample was larger in 19/27 of the male mean measurements and in 22/27 of the female mean measurements. In Table 3, the mean values for males and females of Victoria and Tasmania are listed for the 10 measurements chosen for the *P. nasuta* intraspecific analysis in Part 2 and also for 2 alisphenoid bulla measurements (discussed later). When the various male and female pairs of values for these 12 measurements were compared by t-tests, only 5/24 differences were found to be significant—in males, frontal length, minimum frontal breadth and alisphenoid bulla breadth at the 5 per cent level; in the females, palatal length and minimum frontal breadth at the 1 per cent level. It was therefore felt that multivariate analysis was necessary to determine whether a significant difference could be established between the 2 populations.

Table 4 gives the results of Mahalanobis' D^2 (Rao, 1952) applied to the first 10 measurements listed in Table 3. The results for both males and females are not significant at the 5 per cent level. The test was then re-applied but this time substituting alisphenoid bulla length and breadth (Table 3) for posterior palatal vacuity length and breadth. This substitution was made because of the importance of alisphenoid bulla size in other species of the genus (e.g. *P. bougainville*). For this test, the D^2 value is significant for males at the 5 per cent level (Table 4). Relative to the number of observations, the use of 10 characters results in comparatively few degrees of freedom in the denominator of the F statistic used for testing significance of the D^2 value. Consequently a further D^2 analysis was carried out using only 5 measurements: maximum cranial length, cranial breadth, occipital height, mandibular ramus length and mandibular height. The D^2 values obtained in this analysis are not significant at the 5 per cent level (Table 4). Finally, investigation of the size difference between the 2 populations of *P. gunnii*, using maximum cranial length, cranial breadth and occipital height (as was done in *P. nasuta*), gave a non-significant result.

When the mean values of the 50 tooth measurements of *P. gunnii* for Victoria and Tasmania were compared, it was found that, in the males, 25/50 were larger in the Tasmanian sample and 3 equal in the 2 samples; in the females, 34/50 were larger in the Tasmanian group and 3 again equal. There appeared to be no clear pattern in these results, although all of the mean tooth row measurements were larger in the Tasmanian sample in both males and females, but it was felt that this mainly reflected the greater palatal length in that group. Because of these findings, and the negative results for the skull measurements, no multivariate analysis of tooth measurements in the two examples was made.

2. *P. bougainville* and the central group (plates 33 and 34).

In these specimens, because of the paucity of material, only one sample, *P. bougainville notina* was examined for sexual dimorphism. In Table 5, the results of t-tests on the canine teeth of males and females of this group are listed. The male mean values are larger in 5/6 instances, but only one of the 6 comparisons is significant at the 5 per cent level. It would seem from these results that the 2 sexes differ very little in the measurements of these teeth, which in the previously examined species of the genus differed significantly. For this reason, and because of the small numbers of specimens available, the 2 sexes were considered together in the rest of the analysis.

The samples of *P.b. notina* and *P.b. bougainville* were next compared. Tables 6 and 7 list the numbers of specimens and mean values for the skull and tooth measurements of these 2 samples. Because of the small number of *P.b. bougainville* specimens available, only a pooled standard deviation for each measurement in the 2 samples has been included in the Tables and these values have been used for calculating the t-test values listed. In the skull measurements (Table 6), the *P.b. notina* mean value is larger than that for *P.b. bougainville* in 21/27 instances, but only 4 of these are significant by t-tests at the 1 per cent level and a further 5 at the 5 per cent level. Of interest are the facts that the alisphenoid bulla length and breadth measurements are both significantly different at the 1 per cent level and 3/6 cranial breadth and 2/4 cranial height measurements are also significantly different at either the 1 per cent or 5 per cent level. All of these mean measurements are larger in *P.b. notina*.

In the teeth (Tables 7A and B), the *P.b. notina* mean measurements are larger in 29/51 instances. However, of the 7 measurements which differ significantly by t-tests in the 2 samples at the 1 per cent level, only 4 are larger in *P.b. notina* and of the 4 which differ at the 5 per cent level, 3 are larger in that species. The single striking difference between the 2 groups highlighted by the t-tests of the tooth measurements is the longer length of I^5 in *P.b. bougainville*, which is significantly different in the 2 groups at the 1 per cent level.

The juvenile/immature group of 12 specimens from uncertain localities, the adult group of 4 specimens also from uncertain localities, and the central group of 5 specimens, were next compared with *P.b. notina* and *P.b. bougainville*. Inspection of the mean values for the tooth measurements of the juvenile/immature group, and the skull and tooth mean values of the uncertain adult group and the central group, suggested that, in the first 2 cases there was a close similarity to *P.b. notina*, while in the 3rd this was not clear cut. Because of their immaturity, the skull measurements of the juvenile/immature group could not be used, but study of the individual alisphenoid bullae of the group indicated that, although not yet at maximum size, they were similar in size to those of *P.b. notina*.

A one-way analysis of variance was next performed on the five populations for each of 6 selected measurements. (See Table 8 for the numbers of specimens and mean values of the 3 additional groups.) Pairwise comparisons of the means were then carried out by Scheffe's S method of multiple comparisons (Scheffe, 1959) and the results are given in Table 9. When comparing *P.b. notina* and *P.b. bougainville* by this method there is a significant difference at the 1 per cent level for alisphenoid bulla length and breadth and the length of I^5. The remaining comparisons are not significant. It should be pointed out that the residual variances from the analyses of variance were all larger than the corresponding variances as estimated in Tables 6 and 7 and this indicates that the additional data were more heterogeneous than that of *P.b. notina* and *P.b. bougainville*. It also explains why the occipital height difference between *P.b. notina* and *P.b. bougainville* is significant in terms of the t-test (Table 6), but is not significant in the multiple comparison table (Table 9).

Of the juvenile/immature group, only I^5 length could be compared to the other 4 groups by Scheffe's S method. In these comparisons (Table 9), a significant difference to the *P.b. bougainville* group is found at the 1 per cent level and the other comparisons are all not significant. For the uncertain adult group, all of the 6 selected means could be compared pairwise by Scheffe's S method. Table 9 shows that this group differs significantly from the *P.b. bougainville* group in 3 measurements (alisphenoid bulla length at the 1 per cent level; alisphenoid bulla breadth and occipital height at the 5 per cent level; I^5 length falls just below the 5 per cent level) and only differs from the *P.b. notina* group in one measurement (occipital height) at the 5 per cent level. Despite the apparent affinity of both of these uncertain groups to the *P.b. notina* sample, it was felt advisable not to include them with that group in the statistical analyses.

Still using Scheffe's S method, the group of 5 specimens from the western part of Central Australia is found only to differ from the *P.b. notina* group in maximum cranial length at the 5 per cent level and not to differ significantly in any of the 6 measurements to the uncertain adult group; compared to the *P.b. bougainville* sample, the central group differs in alisphenoid bulla length and breadth at the 1 per cent level and also in occipital height at the 5 per cent level (Table 9). The affinity of this group thus appears to be greater to the *P.b. notina* than to the *P.b. bougainville* group. However, the probable heterogeneity of the group was mooted in Part 1 and for this reason the individual measurements of 3 of the 5 specimens for the 6 features discussed are listed in Table 10. M. 2630 and M. 1575 are juveniles and only a few tooth measurements are known (M. 1575: I^5 length = 0·9 mm). The possible affinities and implications of these specimens will be taken up in the discussion.

DISCUSSION

Comparisons between the male and female skull and teeth measurements of *P. gunnii* have revealed mean size differences in the skull, tooth row, and canine teeth measurements. The male mean measurements were found to be the larger in the

majority of cases, but in some, mainly in the breadth measurements of the cranium, the female mean measurements were larger. In the remaining measurements of the teeth, the male or female mean dimension was larger with about equal frequency. However, few of the above differences (4 in the skull and 19 in the teeth) were significant by the Aspin-Welch test, only the tooth rows and canine teeth showing consistent sexual dimorphism. These results contrast with those found in Part 2 for *P. nasuta*, where almost every male mean value was higher than the female equivalent and where, further, most of the differences were significant by the Aspin-Welch test at the 2 per cent level. In their variances, 9 differences in the skull and 8 in the teeth were significantly different between the sexes of *P. gunnii* by F tests. The equivalent figures for *P. nasuta* were 17 for the skull and 11 for the teeth. Thus, in mean values and variances, considerably less difference was found between the sexes in *P. gunnii* than in *P. nasuta*.

Separate comparisons of *P. gunnii* males and females from Tasmania and Victoria showed the Tasmanian samples to have the larger mean values in the majority of skull measurements. However, of 24 skull differences (12 male and 12 female) examined by t-tests, only 5 gave significant t-values. In the tooth measurements the 2 samples have larger mean values with about equal frequency. Multivariate analysis of various groupings of skull measurements only gave a significant D^2 value in one male comparison. It was suggested above that the lack of significance in the multivariate analyses might in part be due to the relatively few degrees of freedom in the denominator of the F statistic used for testing the D^2 value, but it is never the less clear that the mainland and island populations do not differ greatly, certainly not as much as the northern and southern subdivisions of *P. nasuta* studied in Part 2. It is doubtful whether the northern and southern *P. nasuta* populations merit taxonomic subdivision and there would thus seem to be no support from the present study for making a subspecific distinction between the Tasmanian and Victorian *P. gunnii* populations, despite the geographical isolation in the latter case.

Sexual dimorphism in the skull and tooth measurements of *P. bougainville* is probably of a very low order and in the small samples available was scarcely detectable. It is of interest to note the decrease in sexual dimorphism in the genus from *P. nasuta* to *P. gunnii* to *P. bougainville* which parallels a general size decrease.

In the comparisons of the skull measurements of *P.b. notina* with those of *P.b. bougainville* the situation appears similar to that found when comparing the Victorian and Tasmanian samples of *P. gunnii*. Whilst the *P.b. notina* mean measurements are mostly larger than those of *P.b. bougainville*, relatively few of the differences are significant by the t-test. In the tooth measurements, only the I^5 length appears to be of interest. The differences found between the 2 groups become of taxonomic importance when their pattern and magnitude are examined. The larger alisphenoid bulla measurements and the shorter length of I^5 in *P.b. notina* are significantly different from those of *P.b. bougainville* at the 1 per cent level and the magnitude of these differences is such that on the alisphenoid bulla alone one can separate virtually every one of specimens included in these 2 samples. Further, these differences are re-inforced by a number of significant differences in the cranial breadth and height measurements. This degree of difference is clearly adequate to justify subspecific separation of the 2 groups, as the 75 per cent rule is generally considered stringent enough for subspecific differentiation (Mayr, Linsley, and Usinger, 1953). Specific differentiation of the 2 groups might even be supported, particularly if differences in features other than the skull and teeth are suitably documented. Examination of such features and samples from intervening regions are, however, required before deciding on the most satisfactory taxonomic status for the 2 populations—especially as no mainland specimens of *P.b. bougainville* were available for study.

The juvenile/immature and adult groups of specimens of uncertain localities, anatomically and metrically appear to belong in the *P.b. notina* group. Further, certain scraps of information about locality and taxonomy which accompany some of them, suggest that they probably came from South Australia. However, particularly in view of the similarity found between the central group of specimens and the *P.b. notina* group, it would seem that this material cannot be utilized further at this stage in discussions of the taxonomy of the long-nosed bandicoots.

Finally there remains the group of 5 specimens from the western part of central Australia. This material is clearly inadequate for any definitive assessment of *P. eremiana* or other population(s) linking the 2 samples, *P.b. notina* and *P.b. bougainville*, discussed above, but even the few specimens available indicate certain possibilities. The most northern of these specimens, M. 2630 and its mother M. 2629 (from Well 35, Canning Stock Route, Western Australia) and also C. 213 (labelled "Central Australia"), in their general dimensions and on I^5 length and alisphenoid bulla length and breadth could readily be referred to *P.b. notina*. Of the remaining 2 specimens, M. 1575 is an immature specimen from Gahanda, Western Australia. It has a short I^5 tooth, similar to that of *P.b. notina*, but its alisphenoid bulla, although not yet fully developed, appears to be of the small variety, as seen in *P.b. bougainville*. The last specimen (S. 1753), for which there is some doubt about exact locality, is larger even than the *P.b. notina* specimens in the majority of its measurements. In addition, it has an I^5 length similar to that of *P.b. bougainville* and an alisphenoid bulla comparable in size to that of *P.b. notina*. These latter 2 specimens thus suggest the possible presence of one or more populations in central Australia, which differ from both *P.b. notina* and *P.b. bougainville*.

SUMMARY

(1) 51 male and female specimens of *P. gunnii* from Victoria and Tasmania have been studied for metrical features of the skull and teeth.

(2) Sexual dimorphism in *P. gunnii* is present in the skull, tooth row, and canine teeth measurements, but not in the other teeth. However, only in the tooth rows and canine teeth are the differences consistently significant.

(3) The Tasmanian sample of *P. gunnii* is larger than the Victorian sample in most of the mean skull measurements, but few of these differences reach a level of significance. Subspecific differentiation of the 2 samples is not merited on this data.

(4) 43 male and female specimens of *P. bougainville* (including 5 specimens which came from *P. eremiana* localities) were also examined for metrical features of the skull and teeth.

(5) The sexed material of *P. bougainville* was very limited, but there appears to be little sexual dimorphism in the skull and tooth measurements.

(6) The *P.b. notina* sample from South Australia differed from the *P.b. bougainville* sample from the islands off the central coast of Western Australia in their generally larger mean measurements. The significantly different alisphenoid bulla and I^5 length, the former being larger and the latter smaller in the *P.b. notina* group, warrant at least a subspecific separation of this sample from the *P.b. bougainville* specimens.

(7) The need for further material, especially from central and western Australia, is indicated by a few scattered specimens from these areas which suggest possibly extensive limits for the range of *P.b. notina* and perhaps the presence of one or more other population(s).

ACKNOWLEDGEMENTS

We should like to thank Mrs S. Pulley and Mrs J. Cochrane of the Department of Statistics, University of New South Wales, Sydney, for computing assistance, and Mrs B. King and Miss D. Papo, of the Department of Anatomy, University of Sydney, Sydney, for typing the manuscript.

The computations for this study were carried out on the I.B.M. 1620 of the Duchess Computing Laboratory at the University of New South Wales, Sydney.

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Table 1.—Comparison of *P. gunnii* male and female skull measurements (in mm)

Measurement	Males			Females			F test	A-W test
	N	$\bar{X}$	SD	N	$\bar{X}$	SD		
Cranium—								
(a) length—								
Max.	19	77·12	3·77	16	75·59	2·39	*	ns
Bas.	18	69·82	3·69	16	68·70	2·25	*	ns
Cond.-Bas. ..	18	74·05	3·65	16	72·86	2·25	*	ns
Pal.	18	48·23	2·31	15	47·02	1·83	ns	*
Nas.	17	35·76	2·43	18	34·78	1·34	**	*
Fr.	19	24·90	1·76	18	24·68	1·26	ns	ns
Par.	19	13·06	0·65	17	13·00	0·56	ns	ns
Ant. to I^1 ..	19	2·50	0·27	18	2·44	0·18	*	ns
(b) breadth—								
Ant. to $\underline{C}$ ..	18	8·02	0·55	18	8·03	0·47	ns	ns
At M^2	18	18·76	0·86	18	18·92	0·74	ns	ns
Int.-Orb. ..	18	26·02	1·22	18	26·18	1·00	ns	ns
Min. Fr. ..	19	14·75	0·64	18	14·97	0·67	ns	ns
Bizyg. ..	16	31·37	1·50	16	31·30	0·83	*	ns
Cran.	18	23·16	0·86	16	22·91	0·69	ns	ns
(c) height—								
Ant. to $\underline{C}$ ..	17	6·15	0·46	17	6·13	0·31	ns	ns
Post. to M^4 ..	18	16·91	0·66	19	16·60	0·76	ns	ns
Cran.	18	23·07	1·07	16	22·84	0·63	*	ns
Occip. ..	18	16·93	0·80	16	16·77	0·56	ns	ns
(d) bulla—								
L	19	5·81	0·48	18	5·63	0·33	ns	ns
B	19	6·54	0·34	18	6·38	0·22	ns	*
(e) vacuities—								
A.P. Vac. L. ..	17	9·75	0·85	18	9·53	0·82	ns	ns
P.P. Vac. L. ..	18	9·55	0·72	17	9·14	0·82	ns	ns
P.P. Vac. Br. ..	17	9·94	0·86	17	9·94	0·98	ns	ns
Mandible—								
Max. L.	21	61·48	3·41	19	59·58	1·74	**	**
Ramus L.	21	6·41	0·44	19	6·27	0·30	ns	ns
Br. at M_2	21	2·82	0·22	20	2·82	0·17	ns	ns
Ht. at M_2	21	6·01	0·73	20	5·75	0·36	**	ns

Significance level: F test ** 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** 2 per cent, * = 10 per cent, ns = not significant.

Table 2A.—Comparison of *P. gunnii* male and female upper tooth measurements (in mm)

Measurement	Males			Females			F test	A-W test
	N	$\overline{X}$	SD	N	$\overline{X}$	SD		
I^1 —M^4	19	43·53	1·90	18	42·63	1·22	*	*
I^1 —I^4	19	6·17	0·26	19	6·03	0·25	ns	*
$\underline{C}$ —M^4	19	31·80	1·26	19	31·02	0·61	**	**
M^1—M^4	19	14·55	0·40	21	14·47	0·45	ns	ns
$\underline{C}$ L	19	2·76	0·35	20	2·30	0·26	ns	**
B	19	1·06	0·07	20	0·88	0·08	ns	**
H	19	3·08	0·49	20	2·55	0·31	*	**
P^1 L	23	2·80	0·14	25	2·78	0·11	ns	ns
B	23	0·96	0·05	25	0·94	0·06	ns	**
P^2 L	24	2·82	0·15	25	2·85	0·12	ns	ns
B	24	1·44	0·11	25	1·40	0·10	ns	**
P^3 L	18	3·36	0·24	22	3·33	0·30	ns	ns
B	20	2·13	0·15	20	2·13	0·12	ns	ns
M^1 B	21	2·92	0·09	25	3·00	0·08	ns	**
LB	24	4·56	0·22	24	4·60	0·19	ns	ns
LL	23	2·64	0·14	24	2·67	0·14	ns	ns
M^2 B	22	3·39	0·10	25	3·47	0·09	ns	**
LB	24	4·04	0·14	24	4·01	0·15	ns	ns
LL	24	2·63	0·12	25	2·65	0·66	ns	ns
M^3 B	20	3·79	0·11	23	3·82	0·11	ns	ns
LB	22	3·80	0·26	24	3·66	0·84	ns	ns
LL	21	2·46	0·19	24	2·52	0·15	**	ns
M^4 B	20	2·79	0·24	22	2·71	0·24	ns	ns
LB	21	3·13	0·22	22	3·05	0·19	ns	*
LL	21	1·43	0·12	22	1·45	0·13	ns	ns

Significance level: F test ** = 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** = 2 per cent, * = 10 per cent, ns = not significant.

Table 2B.—Comparison of *P. gunnii* male and female lower tooth measurements (in mm)

Measurement	Males			Females			F test	A-W test
	N	$\bar{X}$	SD	N	$\bar{X}$	SD		
I_1 —M_4	19	42·04	1·84	20	41·25	1·40	*	**
I_1 —I_3	22	5·10	0·27	24	5·10	0·24	ns	ns
$\bar{C}$ —M_4	20	33·03	1·28	20	32·28	0·84	**	**
M_1—M_4	21	15·38	0·37	23	15·33	0·48	ns	ns
$\bar{C}$ L	20	2·30	0·36	20	1·95	0·19	**	**
B	20	0·95	0·09	20	0·84	0·09	ns	**
H	19	2·14	0·26	20	1·92	0·22	ns	**
P_1 L	26	2·76	0·11	25	2·73	0·12	ns	ns
B	26	0·90	0·04	25	0·89	0·06	ns	ns
P_2 L	26	3·23	0·11	25	3·28	0·14	ns	ns
B	26	1·15	0·05	25	1·12	0·07	ns	*
P_3 L	21	3·63	0·36	20	3·67	0·26	ns	ns
B	21	1·45	0·08	22	1·40	0·09	ns	*
M_1 BM..	24	2·02	0·07	25	2·01	0·05	ns	ns
BD	24	2·45	0·10	25	2·47	0·09	ns	ns
L	23	3·71	0·11	25	3·67	0·15	ns	ns
M_2 BM..	25	2·38	0·09	25	2·38	0·08	ns	ns
BD	24	2·77	0·12	25	2·78	0·11	ns	ns
L	23	4·16	0·13	25	4·11	0·17	ns	*
M_3 BM..	26	2·40	0·07	25	2·39	0·07	ns	ns
BD	25	2·52	0·09	24	2·56	0·12	ns	ns
L	24	4·14	0·14	25	4·12	0·13	ns	ns
M_4 BM..	22	2·15	0·10	24	2·16	0·10	ns	ns
BD	22	1·50	0·15	24	1·52	0·10	*	ns
L	21	3·99	0·16	24	4·02	0·18	ns	ns

Significance level: F test ** = 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** = 2 per cent, * = 10 per cent, ns = not significant.

Table 3.—Mean values (in mm) of 12 selected skull measurements in 2 populations of *P. gunnii*

Measurement	Males		Females	
	Victoria N = 7	Tasmania N = 10	Victoria N = 6	Tasmania N = 10
Max. L.	75·31	78·17	74·48	76·46
Pal. L.	46·99	48·76	45·67	47·92
Fr. L.	23·93	25·74	24·12	25·11
Min. Fr. Br.	14·30	14·97	14·43	15·41
Cran. Br.	23·01	23·26	22·70	23·04
Occip. Ht.	16·86	16·98	16·50	16·93
Mand. Ram. L.	6·46	6·24	6·27	6·45
Mand. Ht.	6·11	5·85	5·87	5·84
P.P. Vac. L.	9·73	9·31	8·92	9·43
P.P. Vac. Br.	9·87	9·89	10·15	9·96
Bulla L.	5·81	5·81	5·65	5·61
Bulla B.	6·40	6·72	6·27	6·40

Table 4.—D^2 values for skull measurements of *P. gunnii* males and females, using samples from Victoria and Tasmania

Measurements	Males N = Vict.—7; Tasm.—10	Females N = Vict.—6; Tasm.—10
10 measurements, incl. vacuity ..	16·6	19·1
10 measurements, incl. bulla ..	54·6*	23·2
5 measurements	3·4	1·2

* Significant at 5 per cent level.

Table 5.—Comparison by t-tests of male and female canine teeth measurements in *P. bougainville notina*

	Measurement	t-value	d.f.
$\underline{C}$	L	0·90	7
	B	1·73	8
	H	0·95	7
$\overline{C}$	L	3·28*	7
	B	0·41	8
	H	0·09	7

* Significant at 5 per cent level.

Table 6.—Comparison of *P.b. notina* and *P.b. bougainville* skull measurements (in mm)

Measurement	*P.b. notina* N	*P.b. notina* $\bar{X}$	*P.b. bougainville* N	*P.b. bougainville* $\bar{X}$	Pooled SD	t test
Cranium—						
(a) length—						
Max.	9	58·82	1	56·60	1·22	ns
Bas.	10	52·98	1	50·80	1·06	ns
Cond.-Bas. ..	10	56·11	1	54·30	1·11	ns
Pal.	7	31·57	2	33·65	0·88	ns
Nas.	9	24·39	2	23·55	0·82	ns
Fr.	11	19·57	2	18·40	0·62	*
Par.	10	12·50	2	12·95	0·94	ns
Ant. to I^1	11	2·28	2	2·25	0·16	ns
(b) breadth—						
Ant. to $\underline{C}$ ..	11	5·58	2	5·55	0·62	ns
At. M^2	10	14·12	2	14·15	0·32	ns
Int.-Orb.	7	21·24	2	19·50	0·50	**
Min. Fr.	11	13·14	2	11·70	0·64	*
Bizyg.	8	24·70	2	24·00	0·31	*
Cran.	10	19·14	2	18·00	0·69	ns
(c) height—						
Ant. to $\underline{C}$ ..	10	4·35	2	4·30	0·13	ns
Post. to $\overline{M}^4$ ..	11	13·50	2	13·00	0·25	*
Cran.	10	19·57	1	19·00	0·80	ns
Occip. ..	10	14·28	1	13·40	0·19	**
(d) bulla—						
L	11	8·05	2	5·40	0·39	**
B	11	6·96	2	5·75	0·27	**
(e) vacuities—						
A.P. Vac. L. ..	6	6·53	2	5·80	0·31	*
P.P. Vac. L. ..	7	8·17	1	7·20	0·39	ns
P.P. Vac. Br. ..	7	7·21	2	7·25	0·54	ns
Mandible—						
Max. L.	11	44·50	2	44·05	1·19	ns
Ramus L.	11	4·51	2	4·70	0·22	ns
Br. at M_2	11	2·10	2	2·00	0·16	ns
Ht. at M_2	11	3·98	2	4·10	0·19	ns

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 7A.—Comparison of *P.b. notina* and *P.b. bougainville* upper tooth measurements (in mm)

Measurement	*P.b. notina* N	*P.b. notina* $\bar{X}$	*P.b. bougainville* N	*P.b. bougainville* $\bar{X}$	Pooled SD	t test
I^1 —M^4	12	31·38	2	31·10	0·92	ns
I^1 —I^4	13	4·43	5	4·36	0·16	ns
$\underline{C}$ —M^4	12	23·14	2	23·15	0·70	ns
M^1—M^4	13	10·80	2	10·10	0·30	**
$\underline{C}$ L	13	1·27	2	1·45	0·16	ns
B	16	0·73	5	0·74	0·05	ns
H	13	1·61	2	1·80	0·16	ns
P^1 L	16	2·35	5	2·30	0·10	ns
B	16	0·86	5	0·90	0·05	ns
P^2 L	16	2·37	5	2·42	0·09	ns
B	16	1·04	5	1·14	0·06	**
P^3 L	12	2·63	2	2·60	0·15	ns
B	13	1·62	2	1·60	0·10	ns
M^1 B	16	2·42	5	2·44	0·08	ns
LB	17	3·31	5	3·28	0·15	ns
LL	16	2·04	5	2·00	0·10	ns
M^2 B	16	2·74	5	2·92	0·11	**
LB	16	3·13	5	2·88	0·09	**
LL	16	2·03	5	1·98	0·08	ns
M^3 B	13	3·01	2	3·20	0·12	ns
LB	13	2·88	2	2·65	0·16	ns
LL	13	1·92	2	1·70	0·10	*
M^4 B	12	1·79	2	1·90	0·20	ns
LB	13	2·48	2	2·20	0·21	ns
LL	12	1·08	2	1·10	0·06	ns
I^5 L	14	0·93	5	1·20	0·08	**

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 7B.—Comparison of *P.b. notina* and *P.b. bougainville* lower tooth measurements (in mm)

Measurement	*P.b. notina* N	*P.b. notina* $\bar{X}$	*P.b. bougainville* N	*P.b. bougainville* $\bar{X}$	Pooled SD	t test
I_1 —M_4	13	30·47	2	30·40	0·89	ns
I_1 —I_3	16	3·78	5	3·70	0·14	ns
$\bar{C}$ —M_4	13	24·33	2	24·20	0·66	ns
M_1—M_4	13	11·70	2	11·15	0·31	*
$\bar{C}$ L	14	1·62	2	1·80	0·13	ns
B	16	0·68	5	0·64	0·05	ns
H	14	1·47	2	1·65	0·11	*
P_1 L	15	2·61	5	2·64	0·11	ns
B	16	0·79	5	0·84	0·06	ns
P_2 L	15	2·93	5	2·86	0·08	ns
B	16	1·01	5	1·06	0·07	ns
P_3 L	11	2·67	2	2·70	0·21	ns
B	12	1·11	2	1·10	0·09	ns
M_1 BM	15	1·53	5	1·54	0·05	ns
BD	15	1·90	5	1·76	0·05	**
L	15	2·91	5	2·72	0·12	**
M_2 BM	16	1·84	5	1·80	0·08	ns
BD	16	2·08	5	2·02	0·05	*
L	16	3·06	5	3·00	0·11	ns
M_3 BM	16	1·88	5	1·86	0·06	ns
BD	16	1·94	5	1·92	0·08	ns
L	16	3·04	5	3·08	0·10	ns
M_4 BM	13	1·65	2	1·60	0·10	ns
BD	13	1·15	2	1·20	0·08	ns
L	13	3·09	2	2·85	0·13	ns

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 8.—6 measurements (in mm) of 2 samples of *P. bougainville* and the Central group

Measurement	Juvenile/ Immature N	Juvenile/ Immature $\bar{X}$	Uncertain Localities N	Uncertain Localities $\bar{X}$	Central Group N	Central Group $\bar{X}$
Max. L.	..	..	4	62·22	2	64·50
Cran. Br.	..	..	4	19·40	3	19·33
Occ. Ht.	..	..	4	15·05	3	14·83
Bulla L.	..	..	4	7·38	3	7·70
Bulla Br.	..	..	4	6·65	3	6·97
I^5 L.	12	0·89	3	0·97	4	1·03

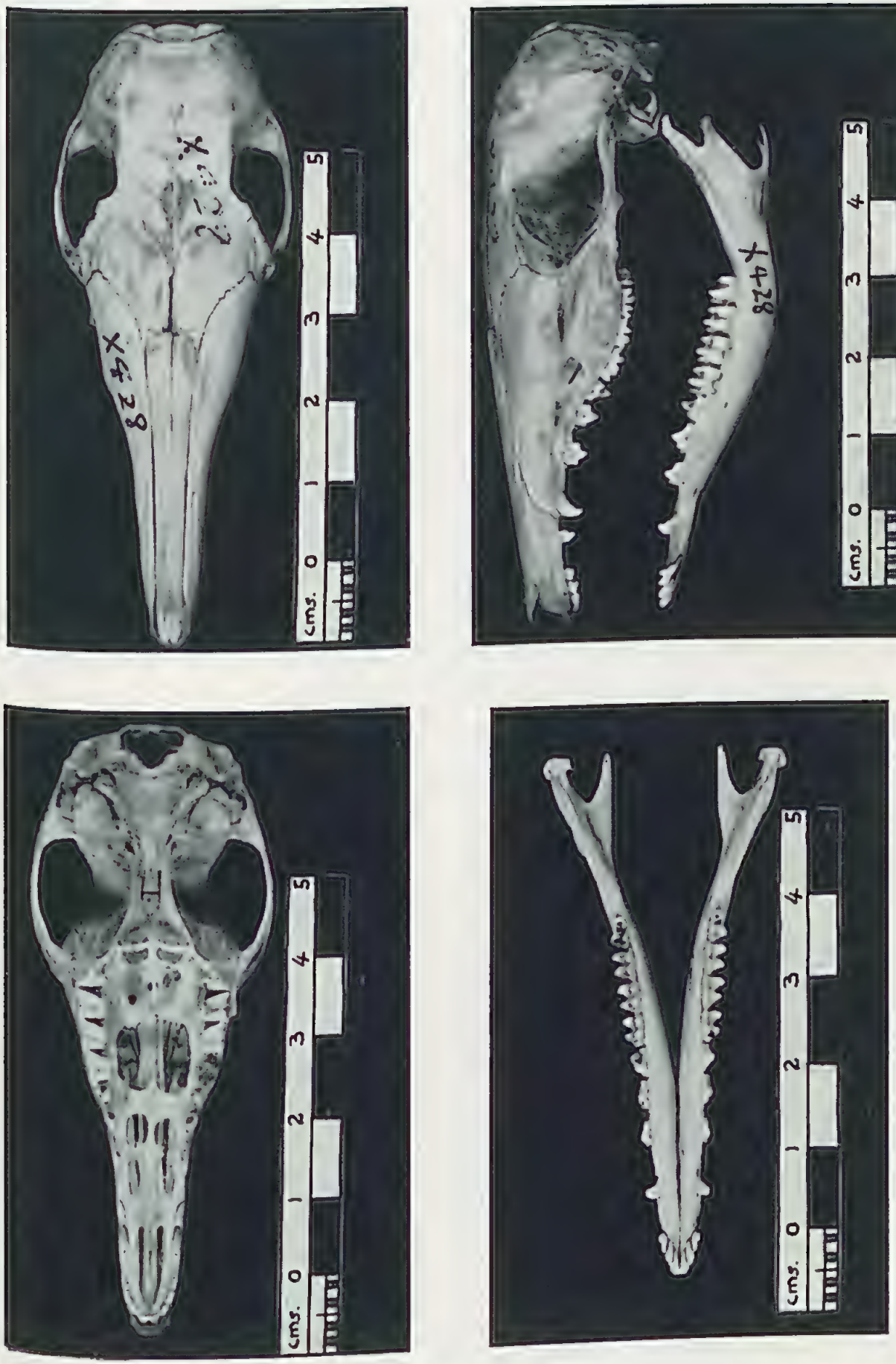
Table 9.—Paired comparisons by Scheffe's S method of 4 samples of *P. bougainville* and the Central group using 6 measurements

Measurement	I-II	I-III	I-IV	I-V	II-III	II-IV	II-V	III-IV	III-V	IV-V	Pooled SD	d.f.
Max. L.	ns	..	ns	*	..	ns	ns	..	..	ns	2·18	12
Cran. Br.	ns	..	ns	ns	..	ns	ns	..	..	ns	0·81	15
Occ. Ht.	ns	..	*	ns	..	*	*	..	..	ns	0·38	14
Bulla L.	**	..	ns	ns	..	**	**	..	..	ns	0·45	16
Bulla Br.	**	..	ns	ns	..	*	**	..	..	ns	0·32	16
I^5 L.	**	ns	ns	ns	**	ns	ns	ns	ns	ns	0·10	33

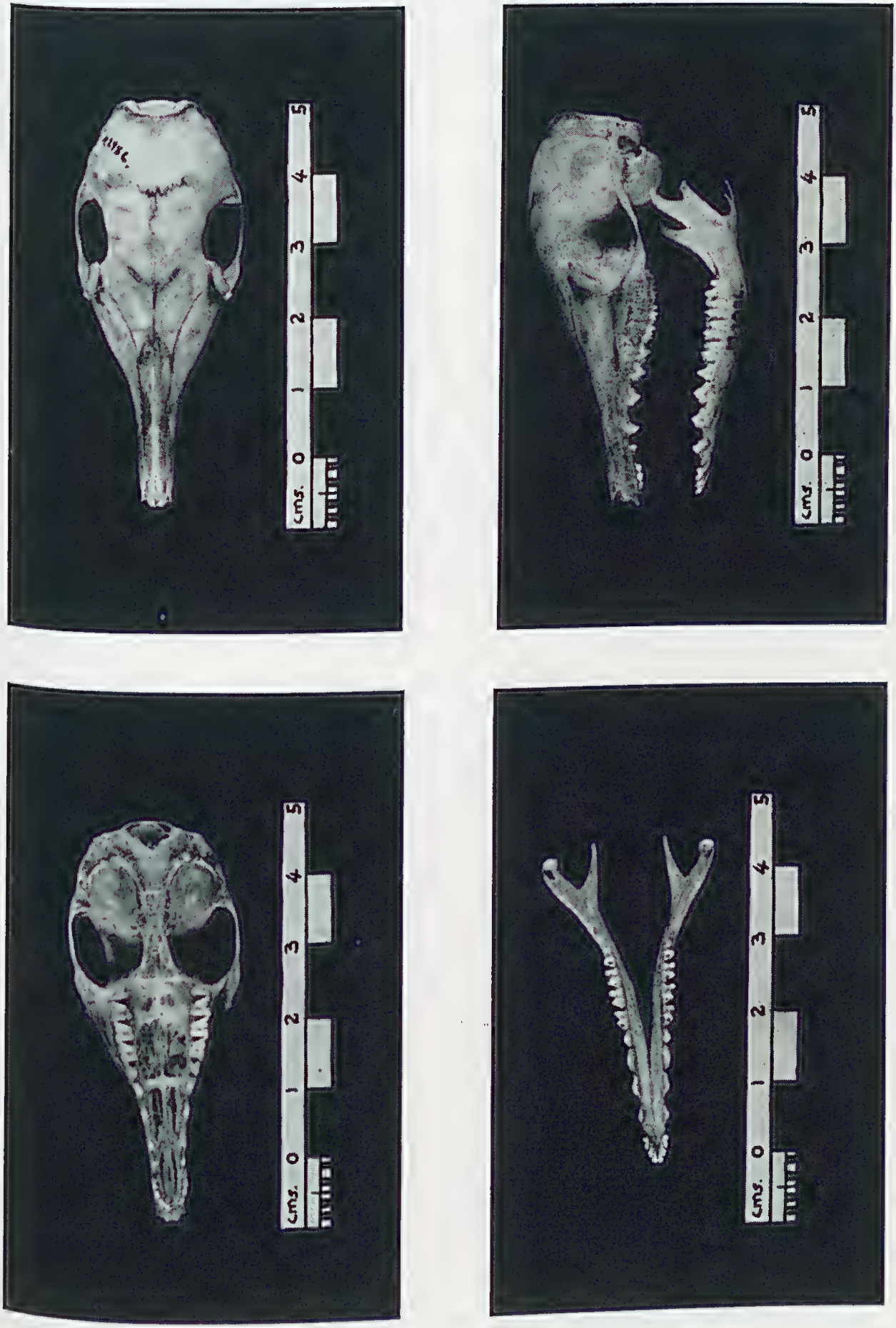
Significance level: ** = 1 per cent, * = 5 per cent, ns = not significant. Key: I = *P.b. notina*, II = *P.b. bougainville*, III = Juvenile/Immature, IV = Uncertain Localities, V = Central Group.

Table 10.—6 measurements (in mm) of 3 Central group specimens

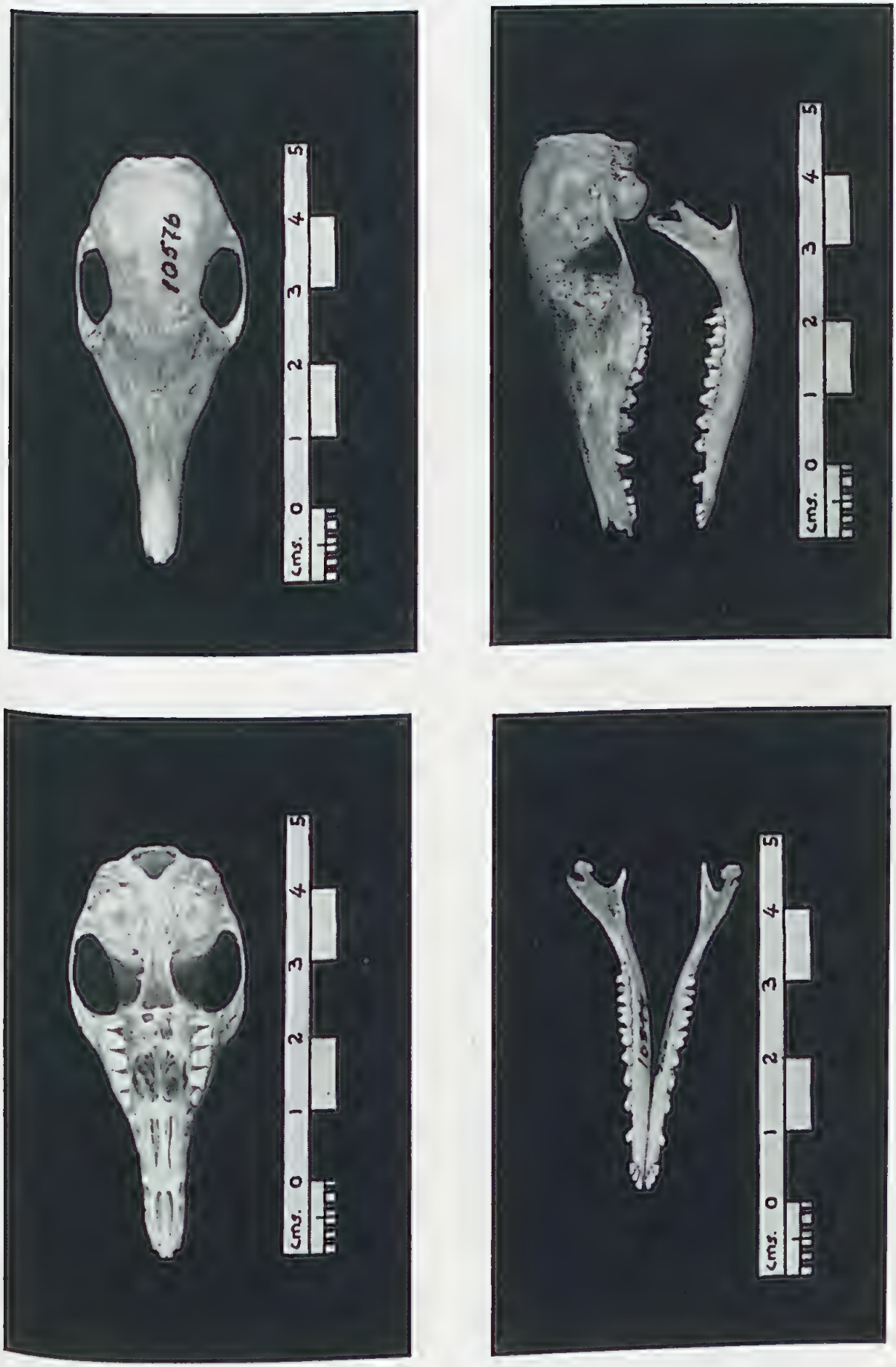
Measurement	S.1753	C.213	M.2629
Max. L.	68·3	60·7	..
Cran. Br.	20·8	18·4	18·8
Occ. Ht.	15·6	14·1	14·8
Bulla L.	7·6	8·3	7·2
Bulla Br.	7·1	7·0	6·8
I^5 L.	1·3	0·9	1·0



Cranium and mandible of *P. gunnii*, male (X.428)



Cranium and mandible of *P.b. nolina*, sex unknown (M.2986)



Cranium and mandible of *P.b. bougainville*, male (10576)

A REVISION OF THE GENUS *OVALIPES* RATHBUN, 1898 (CRUSTACEA, DECAPODA, PORTUNIDAE)

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Plates 35–42. Figures 1–4.

Manuscript received, 15th August, 1966

SUMMARY

Recent workers have recognized five species in the genus *Ovalipes*: *O. ocellatus* (Herbst, 1799), *O. punctatus* (de Haan, 1833), *O. guadulpensis* (Saussure, 1858), *O. iridescens* (Miers, 1886), and *O. molleri* (Ward, 1933). However, five species have been confused under the name of *O. punctatus* and these comprise: *O. punctatus* (de Haan, 1833), *O. trimaculatus* (de Haan, 1833), *O. catharus* (White, 1843), *O. australiensis* n.sp., and *O. elongatus* n.sp. A further new species, *O. georgei*, has appeared in recent collections from Western Australia, and it seems that there may be two forms of *O. guadulpensis*.

The new species are described and the remaining species redescribed. This has necessitated a redescription of the generic features and consideration of the possibility of either dividing the genus into several genera or erecting subgenera. Neither of these possibilities has been followed, but, instead, two groups have been designated (A and B), each with two subgroups. Thus the *O. punctatus* subgroup contains *O. punctatus*, *O. trimaculatus*, *O. catharus*, *O. australiensis*, and *O. elongatus*., and, with the *O. georgei* subgroup comprising only *O. georgei*, makes up Group A. The *O. iridescens* subgroup comprises *O. iridescens* and *O. molleri*, and with the *O. ocellatus* subgroup comprising *O. ocellatus* and *O. guadulpensis* makes up Group B.

The *O. punctatus* subgroup contains shallow-water species primarily from the Indo-West-Pacific area, including *O. punctatus* from Japanese and Chinese waters, and three species from Australasian waters (*O. catharus*, *O. australiensis*, and *O. elongatus*). It also contains one circum-Southern Hemisphere species (*O. trimaculatus*) which has not been recorded from Australasia. The species of the *O. iridescens* subgroup are deeper-water Indo-West-Pacific species, and those of the *O. ocellatus* subgroup are from shallow waters of the Western Atlantic.

Whereas previously only two species were known from Australasian waters, now six are recorded, viz: *O. catharus*, *O. australiensis*, *O. elongatus*, *O. georgei*, *O. iridescens*, and *O. molleri*.

The presence of stridulating structures is a feature of the genus, but it is difficult to understand why each of the subgroups either has a different striated structure or a different structural modification which acts as a plectrum.

I. INTRODUCTION

This investigation commenced with the recognition of a new species of the genus kindly forwarded by Dr R. George, of the Western Australian Museum. Dr George also indicated his belief that specimens in his museum collection previously identified by the senior author as *Ovalipes punctatus* comprised more than one species. Re-examination of his material and specimens borrowed from numerous institutions confirmed that several closely related species had been synonymized by all recent workers, following Rathbun (1930). Sighting of South Atlantic material in American

institutions by the senior author, and examination of loaned specimens by both authors, showed that one species in this closely related group was common to the Indian, Pacific, and Atlantic Oceans.

As will be shown in a later section, while *Ovalipes* Rathbun (1898) is a valid genus, it is readily divisible into four sub-groups. The relationships between the species within each sub-group are very close, but the differences between the sub-groups are not great enough to merit subgeneric status. The sub-groups are as follows: *O. punctatus* sub-group, containing *O. punctatus*, *O. trimaculatus*, *O. australiensis*, *O. elongatus*, and *O. catharus*; *O. georgei* sub-group, containing only *O. georgei*; *O. iridescens* sub-group, containing *O. iridescens* and *O. molleri*; and *O. ocellatus* sub-group, containing *O. ocellatus* and *O. guadulpensis*. The order in which the descriptions of the species are presented below follows the order of sub-groups just given.

Detailed study of the various species has revealed several features of diagnostic importance which have not been used in previous studies on the genus. These include the details of the different segments of the three pairs of walking legs, in which the terminology of orientation presents problems. Because of their curvatures and different angles of attachment to the body, the terms "anterior" and "posterior", and "upper" and "lower", would cause confusion. Orientations are referred to the "outer border" which is the outer surface of curvature of the limb. The shapes and relative hirsuteness of the meri of the third maxillipeds are also of diagnostic importance, with obvious differences in the shape of the anterointernal angle. Within the genus there are three main kinds of stridulatory structures and the differences between them are important at subgroup and species levels. It is hoped to consider the functional morphology of these structures in a later paper, supplementing the work of Guinot-Dumortier and Dumortier (1960).

All carapace breadth measurements are to the nearest mm. In determining breadth/length ratios of the carapace, the measured length was the distance between the most posterior part of the frontal border (i.e., between median and lateral frontal teeth) and the centre of the posterior border of the carapace. All drawings are from camera lucida outlines.

The following abbreviations have been used in the text: AM—Australian Museum, Sydney; CM—Canterbury Museum, Christchurch; DMNZ—Dominion Museum, Wellington; MCZ—Museum of Comparative Zoology, Harvard; MM—Macleay Museum, University of Sydney; NM—National Museum of Melbourne; QM—Queensland Museum, Brisbane; QVM—Queen Victoria Museum, Launceston; S Afr M—South African Museum, Natal; S Aust M—South Australian Museum, Adelaide; USNM—United States National Museum, Smithsonian Institution, Washington; UZM—Universitetets Zoologiske Museum, Copenhagen; WAM—Western Australian Museum, Perth; ZMA—Zoologisch Museum, Amsterdam. In cases where the abbreviation is followed by a number, or letters and a number, these are the museum's registration numbers.

In the "Material Examined" sections, continents are arranged from west to east; within continents, countries and states are arranged from north to south; and within countries and states, the arrangement is chronological.

II. GENERIC SYNONYMY

The synonymy below does not include all usages of the different names by which this genus has been known; for this, specific synonymies later in the paper should be consulted. It includes first usages and a selection of the more important later ones.

Genus **Ovalipes** Rathbun

Platyonichus Latreille, 1825, p. 151. (Type species: *Cancer ocellatus* Herbst, 1799).

non *Platyonichus* Latreille, 1818, p. 4. (emend pro *Portumnus* Leach, 1814).

Anisopus de Haan, 1833, pp. 3, 12. (Type species: *Corystes* (*Anisopus*) *punctata* de Haan, 1833).

non *Anisopus* Meigen, 1803, p. 264. (Diptera).

Platyonychus Voigt, 1836, p. 104. Dana, 1851, p. 130. Miers, 1886, pp. 201–2.

Ovalipes Rathbun, 1898, p. 597; (Type species: *Cancer ocellatus* Herbst, 1799); 1930, pp. 18–19. Sakai, 1939, p. 374. Barnard, 1950, p. 150. Stephenson and Campbell, 1960, pp. 88–9. Crosnier, 1962, p. 20. Garth and Stephenson, 1966, p. 12.

Aeneacancer Ward, 1933, p. 381. (Type species: *Aeneacancer molleri* Ward, 1933). McNeill, 1953. p. 93.

III. GENERIC DESCRIPTION

The discovery of new species, and particularly *O. georgei*, necessitates redescription of the genus.

Front: Rather narrow, armed with three or four lobes or teeth (counting inner supraorbital angles as lateral frontal lobes.) In most species subsidiary lateral frontal lobes present, either beneath lateral frontal lobes or median to them forming incipient submedian lobes.

Orbit: Fairly widely open dorsally, with one or two supraorbital notches; one suborbital notch, and well developed suborbital tooth. Eyes moderately long.

Basal joint of first antenna: Short, not filling orbital hiatus, not fused distally with front.

Basal joint of second antenna: Often visible dorsally, frequently flat dorsally, sometimes flat area iridescent.

Anterolateral teeth: Five, approximately equal in size and spacing.

Carapace: Relatively narrow (breadth/length ratio from 1.2 to c. 1.35) (excluding specimens narrower than 18 mm breadth) and deep dorso-ventrally; anterolateral borders curved; dorsal surface convex, without tubercles (except *O. georgei* and to a lesser extent *O. punctatus*) and without transverse ridges (oblique postlateral ridges in *O. georgei*).

Chelipeds: Usually subequal. Arm—without spines on posterior border, boss on anterodistal margin. Wrist—with well developed internal spine. Hand—boss on proximal portion of upper surface at wrist articulation; upper surface with three carinae, innermost conspicuous and ending in a spine, outermost also conspicuous; outer surface carinate in most species; under surface in some species with conspicuous striae; inner surface dorsally with dense row of hairs, carinae generally visible in centre of palm. Moveable finger—carinate on inner and outer edges of upper surface with dense row of bristles just below inner carina.

Walking legs: First leg: dactyl in females long, sharp, with flattened grooved surfaces and carinate edges; this also applies to males, except those in Group A, which are triradiate in section. Propodus carinate on outer border (some species with bifurcate carina); carpus with two carinae or smooth ridges on outer border. Second leg: dactyl, as for first leg (except in *O. iridescens* subgroup); propodus with carina on outer border (some species with carina tending to be bifurcate); carpus carinate, bicarinate or with rounded ridge on outer border. Third leg: dactyl as for second leg; propodus and carpus with carinate outer border.

Fifth leg: Dactyl flattened, enlarged and oval shaped; propodus enlarged and flattened; carpus with anterior border sharp and either hirsute or forming a carina; merus broad.

Third maxillipeds: Large; ischium not produced at anterointernal angle; merus with upper surface bearing long hairs in most species and with raised ridge in posterointernal area, anteroexternal angle rounded or obliquely angled, anterointernal angle distinctly produced (except in *O. catharus*).

Male abdomen: Ultimate segment broader than long, sometimes distinctly so, and indented into penultimate segment either slightly or extensively.

Male pleopod: Relatively short and robust; inner side smoothly curving; both sides abundantly beset with long, bipinnate hairs and bearing subterminal spinules; extreme tip bare.

Stridulating ridges: Present either on under surface of hand of chelipeds, or on pterygostomial region or postlateral region of the carapace.

Colour: In alcohol-preserved specimens which retain their colour, most species possess *either* two red postlateral marks *or* alternatively iridescence on some part of carapace (except for *O. elongatus* and *O. georgei*).

IV. KEY TO SPECIES OF THE GENUS OVALIPES

1		Striae present on under surface of hand of cheliped (*O. punctatus* sub-group)	2
..		Striae present on mesobranchial area of carapace.....	*O. georgei*
..		Striae present on pterygostomial area of carapace	6
2	(1)	Coarse granules on carinae on upper surface of hands.....	3
..		Fine granules on carinae on upper surface of hands	4
3	(2)	Anterior surface of carapace finely granular	*O. punctatus*
..		Anterior surface of carapace coarsely granular	*O. australiensis*
4	(2)	Striae on under surface of hand (excluding under surface of immovable finger) fine, typically 26 or more present	*O. trimaculatus*
..		Striae on under surface of hand (excluding under surface of immovable finger) only moderately fine, typically 26 or less present ..	5
5	(4)	Carapace broad (B/L 1.37)	*O. catharus*
..		Carapace relatively elongate (B/L 1.23)	*O. elongatus*
6	(1)	Posterior area of carapace with two conspicuously thin areas of cuticle (*O. iridescens* sub-group)	7
..		Posterior area of carapace without conspicuously thin areas of cuticle (*O. ocellatus* sub-group)	8
7	(6)	Three frontal teeth	*O. iridescens*
..		Four frontal teeth	*O. molleri*
8	(6)	Frontal teeth relatively blunt, carapace covered with small rings of pigment	*O. ocellatus*
..		Frontal teeth relatively sharp, carapace without small rings of pigment	9

9 (8) Upper surface of hand of cheliped between carinae densely granular, mostly fine, but with occasional large granules *O. guadulpensis*, form a.

Upper surface of hand of cheliped moderately finely and densely granular ..... *O. guadulpensis*, form b.

V. DESCRIPTIONS OF SPECIES

Ovalipes punctatus (de Haan)

Pls 35A, 38A, 38B, 42A; figs 1A, 2A, 3A, 4A

Corystes (*Anisopus*) *punctata* de Haan, 1833, p. 13; 1835, p. 44; pl. 2, figs 1–1d.

Anisopus punctatus de Haan. Stimpson, 1858, p. 39; 1907, p. 86.

Ovalipes punctatus (de Haan). Sakai, 1939, pp. 374–5; pl. XLII, fig. 3 (coloured); 1965, pp. 112–3; pl. 50, fig. 3 (coloured).

non *Ovalipes punctatus* Rathbun, 1930, pp. 24–7, pls 5–8. Porter, 1936a, p. 142; 1936b, p. 337. Crane, 1937, p. 66. Barnard, 1950, pp. 150–2, figs 27a, 29a–d. Garth, 1957, p. 35. Fagetti, 1960, pp. 148–50; pl. III, figs 1–9. Crosnier, 1962, p. 21, fig. 25. Garth and Stephenson, 1966, pp. 12–14; pl. I, figs A–D; pl. XII, fig. A.

= *O. trimaculatus* (de Haan).

non *Ovalipes punctatus* Stephenson and Campbell, 1960, pp. 89–90, figs 1C, 2E; pl. 2, fig. 2; pl. 5E.

= mostly *O. australiensis* n. sp.; Lord Howe I. specimens = *O. elongatus* n. sp.

Material examined:—

Japan: 3 ♂♂ (71, 74, 94 mm), off E. coast of Niphon (sic), North Pacific Exploring Exped., Capt. John Rogers, U.S.N., USNM 2038, ident. by W. Stimpson as *Anisopus punctatus* and by M. J. Rathbun as *Platyonychus bipustulatus* and then *Ovalipes punctatus*. 2 ♂♂ (25, 31 mm), ♀ (fragmented) H. Loomis, USNM 17561. ♂ (84 mm), Same, Rikuoku, Jordan and Snyder, 1900, USNM 26256, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. 2 ♂♂ (18, 24 mm), 5 ♀♀ (23–44 mm), Yenoshima, USNM. ♂ (76 mm), Sibushi, Osumi, Kiusiu I., coll. T. Urita, USNM 48327. 2 ♀♀ (29, 35 mm), Toyama Bay, Honshu, don. Hokkaido Imp. Univ., coll. Madoka Sasaki, 1925, USNM 60248, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (82 mm)*, Oshoro, don. Hokkaido Imp. Univ., coll. Madoka Sasaki, USNM. ♂ (95 mm), ♀ (69 mm), Japan, coll. I. Kubo, WAM 37–63. ♂ (50 mm), (damaged), Hayama Beach, Sagami Bay, 10/ix/1966, I. Bennett.

China: ♂ (86 mm), Foochow, coll. C. R. Kellogg, 1924, USNM 58727, ident. M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (87 mm), Foochow, taken by Foochow fishermen, don. S. F. Light, USNM 61976, ident. M. J. Rathbun as *Ovalipes punctatus*.

Japan or China: ♂ (25 mm), U.S.S. "Palos" Sta. 2325, Dale and Jouy, USNM 5284.

Japan: Incomplete specimen, probably this species: ♀ (57 mm), Hakodate, "Albatross", 19/ix/1897, USNM 20178, prev. ident. as *Xaiva bipustulata*, and by M. J. Rathbun as *Ovalipes punctata*.

Material illustrated: ♂ (82 mm), see * above.

Description:—

Front: Four toothed (including inner supraorbital lobes); teeth roughly equally spaced; medians moderately blunt and produced further forwards than laterals; median fissure deep; lateral teeth fairly sharp; subsidiary lateral lobe on lower plane than lateral tooth, relatively small, hirsute, with line of granules, and visible dorsally on inner side of lateral tooth.

Orbit: Upper border toothed; inner supraorbital notch deep; outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: Without flattened dorsal area; clearly visible dorsally; upper surface sparsely hirsute.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five; distinctly large and robust; broad based and narrowly separated; bordered by coarse granules; first tooth blunter than second and stout, truncate with broad base; fourth the largest; fifth the smallest and sharpest.

Carapace: Broad (B/L 1.33); areas generally not distinct although with distinct cervical grooves; anterior granulation fairly coarse, posterior granulation fine, almost smooth in cardiac region; central protogastric area sometimes bearing one or two inconspicuous tubercles; pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, subequal. Arm-anterior border without spines or tubercles; anterodistal border with large boss; posterior border coarsely and densely granular and distinctly hairy; under surface finely granular tending squamiform. Wrist—with long, robust inner spine; upper surface with small sharp tubercle at hand articulation, covered with fine dense granules, and bearing two indistinct carinae; outer surface with indistinct finely granular carina. Hand—not swollen, upper surface with boss at wrist articulation and with three distinct carinae, the innermost ending in a small sharp spine; between carinae, sparsely scattered fine granules; inner surface generally smooth with two distinct, coarsely granular central carinae, and with upper border densely fringed with hairs; under surface with 13–20 coarse, deep striae; outer surface dorsally almost smooth with fine scattered granules, with below two distinct granular carinae, the more dorsal coarsely granular and the more central finely granular. Moveable finger—upper surface bearing three carinae of spiniform granules; inner surface with an almost smooth carina below dense fringe of hairs; outer surface with finely granular carina. Immovable finger—inner surface with two distinct granular carinae and two scattered rows of hairs; outer surface with two distinct granular carinae. Both fingers—robust, with fairly sharp tips and blunt teeth.

Walking legs: Males with first leg modified—dactyl triradiate in section, distal part of merus with conspicuous raised collar. First leg: propodus with granular carina on outer border; carpus with two granular carinae on outer border. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with partly granular carina on outer border; carpus with two granular carinae on outer border and short granular carina near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus with almost smooth carina on outer border; carpus with partly granular carina on outer border and distally a short rounded ridge near outer surface.

Fifth leg: Carpus with sharp hirsute anterior border; merus broad (L/B 1.76).

Merus of third maxilliped: Surface covered anteriorly with moderately dense long hairs and without conspicuous granules; anterointernal angle slightly produced; anteroexternal angle slightly produced laterally; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment—broader than long, tip rounded; posterior border slightly curved not deeply indented into penultimate segment; penultimate segment—slightly broader than long, sides convex.

Male first pleopod: Evenly curving and tapering towards tip, without broad basal portion. Outer side—dense double row of bipinnate hairs on proximal two-thirds becoming scattered and terminating behind tip, also bearing narrow band of tubercles terminating almost at tip. Inner side—dense row of bipinnate hairs on proximal two-thirds and second scattered row closer to tip, row of microscopic spinules present beginning at level of second row of hairs and terminating behind tip.

Colour

(a) *Alcohol preserved material.* When after prolonged preservation reddish pigment is visible, it is distributed as follows: carapace—borders of frontal and antero-lateral teeth, small spots on anterior half of carapace, metagastric area with transverse patch; chelipeds—general upper and inner surface of arm, boss on arm at wrist articulation, granules on upper surface of wrist, granules on upper surface of hand, tubercles on hand at wrist and outer finger articulations, ventral half inner surface hand, proximal granules on upper surface moveable finger, proximal two-thirds of inner surface of movable finger, ventral portion of outer surface movable finger, and proximal dorsal portion of inner surface of immovable finger.

(b) *Dried material* A male at the Smithsonian Institution (USNM 48327) differs from the above in: stronger pigmentation throughout, predominantly orange-red, conspicuous small spots over all carapace except H-shaped mark near cervical grooves; anterior branchial regions each with a concentration of spots and posterior branchial areas with distinct patches with diffuse borders.

(c) *Fresh material.* This species has not been seen alive by the authors. Sakai (1939, 1965) gives two distinctly different coloured plates of this species. The first (1939, pl. XLII, fig. 3) suggests a recently caught specimen and is predominantly deep-purple in colour with: darker edges to carapace, carapace generally with small dark spots on pale ground, spots concentrated on each anterior branchial region, H-shaped pale mark in region of cervical grooves surrounded by denser pigmentation. His second plate (1965, pl. 50 fig. 3), although stated in his preface to be from a living specimen, greatly resembles the general colour of the dried specimen described in (b) above. It differs from this mostly in having the outer borders of the pale H mark marked with denser pigment, and in having a row of small rings of pigment marking the anterior border of the branchial region.

Stimpson (1907, p. 86) gives colour in life as "reddish, from clouds of reddish-brown punctae. Carapax with a clear blue spot at each posterior corner; also a W-shaped blue spot, with a dark-red patch in front of it, at the middle." This has similarities to Sakai's (1939), pl. XLII, fig. 3.

Distribution

Japan (de Haan, 1833, 1835; Sakai, 1939, 1965), and now China.

Remarks

In its pigmentation the dried specimen of this species and Sakai's (1965) plate show closest resemblance to *O. catharus* but differ in having much more feebly developed anterior carapace patches.

It is characterized by the coarse granulation of the carinae on the upper and outer surfaces of the hands of the chelipeds, and by the coarse, deep, striae on the under surfaces of the hands.

Dr L. B. Holthuis has kindly provided photographs of the lectotype of de Haan's *Corystes* (*Anisopus*) *punctata*. It is a male, Rijksmuseum van Natuurlijke Historie, Leiden, "Reg. No. Crust. D. 365, Japan, 1823–1830, leg. P. F. von Siebold, alcohol specimen". The breadth of the carapace from the natural-size photograph is 51 mm.

Ovalipes trimaculatus (de Haan)

Pls 35B, 38C, 38D, 42B; figs 1B, 2B, 3B, 4B

Corystes (*Anisopus*) *trimaculata* de Haan, 1833, p. 13.

Platyonichus bipustulatus H. Milne Edwards, 1834, p. 437, pl. 17, figs 7–10. de Haan, 1835, p. 44. Milne Edwards and Lucas, 1844, p. 22. Nicolet, 1847, p. 148.

Anisopus trimaculatus de Haan. Macleay, 1838, p. 62. Krauss, 1843, p. 27.

Platyonychus bipustulatus H. Milne Edwards. White, 1847, p. 42. Bell, 1853, pp. 83–4. A. Milne Edwards, 1861, p. 413. Miers, 1881, p. 68. Pfeffer, 1890, p. 546. Ortmann, 1893, p. 65. Lenz, 1902, p. 757.

Platyonychus purpureus Dana, 1852, p. 291; 1853, p. 1593; 1885, pl. 18, figs 3a, 3b. (fide Rathbun, 1930, p. 24, and her plate 5). Cunningham, 1871, p. 492.

Platyonychus africanus A. Milne Edwards, 1861, p. 413, pl. 34, figs 2, 2a.

Ovalipes bipustulatus (H. Milne Edwards). Rathbun, 1898, p. 597; 1910, p. 577. Porter, 1903, p. 149; 1905, p. 32; 1925, p. 317.

non *Ovalipes bipustulatus* Hale, 1927, pp. 147–8, fig. 148 = *O. australiensis* n. sp.

Ovalipes trimaculatus (de Haan). Stebbing, 1902, p. 23. Doflein and Balss, 1912, p. 38.

non *Ovailipes trimaculatus* (sic) Fulton and Grant, 1906, p. 18 = *O. australiensis* n. sp.

Ovalipes punctatus Rathbun, 1930, pp. 24–7 (in part), pls 5–8. Porter, 1936a, p. 142; 1936b, p. 337. Crane, 1937, p. 66. Barnard, 1950, pp. 150–2, figs 27a, 29a–d. Garth, 1957, p. 35. Fagetti, 1960, pp. 148–50, pl. iii, figs 1–9. Crosnier, 1962, p. 21, fig. 25. Garth and Stephenson, 1966, pp. 12–14, pl. I, figs A–D; pl. XII, fig. A.

non *Ovalipes punctatus* Stephenson and Campbell, 1960, pp. 89–90, figs 1C, 2E, pl. 2, fig. 2, pl. 5E = mostly *O. australiensis* n. sp.

Notes on Synonymy

De Haan's (1833) original description states "COR. (ANISOPUS) PUNCTATA *Faun. Jap.*—TRIMACULATA n. sp. (Seba T. XVIII. fig. 9) *Dr Horstok a littore Promontorii Bona Spei.*—? OCELLATA Herbst T. XLIX. fig. 4". Rathbun (1930, p. 24) states that de Haan's *C.* (*Anisopus*) *trimaculata* is a *nomen nudum* because Seba's plate does not illustrate this species. It is here argued that de Haan's name is acceptable because:

(a) *O. trimaculatus* is the only species of the genus known from the Cape of Good Hope.

(b) de Haan (1835, p. 44) obviously refers to the same material as in his original description viz. "*ex. Promontorio Bonae Spei cura Clar. Horstok accepta*", and notes its difference from *O. punctatus* in: "*thorace postice maculis duabus sanguineis notato*". Unfortunately he assigned this material to *Platyonichus bipustulatus*, Milne Edwards.

(c) Drs Holthuis and Sivertsen (in MS) have selected a lectotype for the species. Dr Holthuis has kindly provided photographs of this specimen of *Corystes* (*Anisodon*) *trimaculata*. It is a male, Rijksmuseum van Natuurlijke Historie, Leiden, "Reg. No. Crust. D. 18484, Cape of Good Hope, 1825–1833, H. B. van Horstok, dried specimen". The carapace breadth from the natural-size photograph is 49 mm.

In response to a request for Milne Edwards' type material Dr Danièle Guinot, of the Museum National d'Histoire Naturelle, has kindly lent a male (c. 48 mm) labelled "*Ovalipes bipustulatus* Edw. Ocean Indien ("*Platyonichus bipustulatus*"), Ancienne collection sèche, D. Guinot, nov. 1965". This specimen undoubtedly belongs to *O. trimaculatus* (de Haan). Although lacking any trace of pigment, it agrees with the present species in the following: the shape of the front, anterolateral teeth, carapace granulation, posterolateral borders, cheliped granulation, number and general appearance of striae beneath the hand of the cheliped. The merus of the third maxilliped is slightly damaged but appears to resemble most closely that of *O. trimaculatus*.

Milne Edwards' (1834) coloured plate shows the three characteristic large colour blotches of *O. trimaculatus*, but differs in a much narrower carapace, the form of the merus of the third maxilliped and in having a short stout spine on the inner border of the wrist. This last difference also applies to the present specimen, but the first two appear to be due to imperfections in the draughtsmanship of his figures.

Material examined:—

South Africa. Cape of Good Hope: Damaged specimen (c. 44 mm), Cape of Good Hope, MM.

Capetown: 5 ♂♂ (41–58 mm), 4 ♀♀ (34–48 mm), U.S. "Eclipse" Exped. no. 557, USNM 14882.

Western America. Peru: ♂ (99 mm), Independencia Bay, 1919 don. Brooklyn Mus., coll. Robert Cushman Murphy, USNM 54213, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (58 mm), Paraca Bay, "Haseler" Exped. MCZ no. 5455 USNM 80669, ident. by Walter Faxon as *Ovalipes punctatus*. Juv. (22 mm), U-02298, Chilca Bay, 76° 48′ W., 12° 29′ 30″ S., 17/iii/1941, beach seine, USNM. 5 ♂♂ (42–72* mm), 2 ♀♀ (60, 67 mm), U-02354, data as above. ♂ (99 mm), 2 ♀♀ (77, 87 mm), San Juan Bay, 21/iii/1941, southside, beach seine, USNM.

Chile: 4 ♂♂ (42–45 mm), 2 ♀♀ (53, 82 mm), Lota, Sta. Feb. 15, "Albatross", 1887–88, USNM, 22049, ident. by M. J. Rathbun as *Ovalipes bipustulatus*, then *Ovalipes punctatus*. 5 ♂♂ (45–62 mm), Tome, Feb. 20, "Albatross", 1887–88, USNM 22048, ident. by M. J. Rathbun, as *Ovalipes bipustulatus*, then *Ovalipes punctatus*. Ovig. ♀ (92 mm), Bahia Cumberland, Juan Fernadez Is., coll. W. L. Schmitt, don. Rathbone-Bacon Scholarship, 19/xii/1926, seine haul, beach, USNM 61020, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. 4 ♂♂ (54–69 mm), 4 ♀♀ (59–64 mm), Juan Fernandez Is., coll. W. L. Schmitt, don. Rathbone-Bacon Scholarship, 1926, USNM 61021, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (100 mm), Lota, coll. W. L. Schmitt, don. Rathbone-Bacon Scholarship, 16/i/1927, USNM 61022, ident. M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (54 mm), Chile, coll. Silvestri, don. Buenos Aires Museum, USNM 61073, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. ♂ (110 mm), Chanaral I., 29° 2′ S., 71° 34′ W., coll. W. L. Schmitt, 14/x/1944, U-42-249, trawl net, "Jaira", USNM 81056. ♂ (37 mm), Guayacan Bay, Port Herradura, 29° 59′ S., 71° 22′ 30″ W., 15/x/1944, U-42-264, beach seine, USNM 81054, ident. by W. L. Schmitt as *Ovalipes punctatus*. Ovig. ♀ (111 mm), Quellon, Chiloe I., 43° 8′ S., 73° 31′ W., 2/ii/1945, U-42-400, trammel net, "Jaivas", USNM 81055, ident. by W. L. Schmitt as *Ovalipes punctatus*.

Previously unrecorded specimens are listed in Garth and Stephenson (1966). They comprise: ♂ (25 mm), Papudo, R. Paessler, ex. Hamburg Museum, K. 2612. ♀ (35 mm), Antofagasta, 27/vii/1914, R. Paessler, ex. Hamburg Museum, K. 5244. *Eastern America. Uruguay:* ♂ (80 mm), Cabo Santa Maria, Rocha, coll. Florentino Felippone, USNM 54632, ident. by M. J. Rathbun as *Ovalipes punctatus*.

Argentina: ♂ (48 mm), Chubut, La Plata, exch. La Plata Museum, Feb. 1896, AM G 1331. ♂ (11 mm), Golfo Neuvo Chubut, coll. Independencia, don. Buenos Aires Museum, USNM 61019, ident. by M. J. Rathbun as *Ovalipes bipustulatus*. ♀ (56 mm), Mar del Plata R., coll. and don F. Felippone, 1928?, USNM 62365, ident. by M. J. Rathbun as *Ovalipes punctatus*. ♀ (28 mm), Mar del Plata, don F. Felippone, USNM 62475, ident. by M. J. Rathbun as *Ovalipes punctatus*.

Patagonia: ♂ (69 mm), ♀ (65 mm), Puerto Madryn, don. Buenos Aires Museum, 1915, USNM 61018, ident. by M. J. Rathbun as *Ovalipes bipustulatus*.

Tristan da Cunha: ♂ (86 mm), G. J. Broekhuysen, 1948, M. 186, Rijksmuseum van Natuurlijke Historie, Leiden. (Through the kindness of Dr L. B. Holthuis). ♀ (77 mm), Tristan da Cunha, University of Capetown, Ecological Survey, M. 186, Kgl. Norske Videnskabers Selskab. (Through the kindness of Dr E. Sivertsen.)

Material illustrated: ♂ (72 mm) Peru, U-02354, see * above.

Description:—

Front: Four-toothed; median teeth close together, short, broadly separated from and produced further forwards than laterals; median fissure deep; lateral teeth fairly sharp; subsidiary lateral lobe on lower plane than lateral tooth, relatively large, hirsute, with few granules and visible dorsally on inner side of lateral tooth.

Orbit: Upper border toothed; inner supraorbital notch deep, outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: Without flattened dorsal area, partly obscured dorsally by subsidiary lateral frontal lobe, upper surface hirsute.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five, distinctly large and robust, broad based and narrowly separated, bordered by moderately coarse granules; first tooth blunter than second, sharp with relatively narrow base; fourth the largest; fifth, the smallest and sharpest.

Carapace: Broad (B/L 1.36); areas generally not distinct, although with distinct cervical grooves; granulation fine throughout, but slightly coarser anteriorly; pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, subequal. Arm—anterior border without spines or tubercles; anterodistal border with large boss; posterior border coarsely and densely granular and distinctly hairy; under surface finely granular, tending squamiform. Wrist—with long, robust inner spine; upper surface with inconspicuous tubercle at hand articulation, covered with fine, moderately dense granules, and with traces of one carina; outer surface with indistinct finely granular carina. Hand—slightly swollen, upper surface with boss at wrist articulation and with three distinct carinae, the innermost ending in a spine, between carinae microscopically granular; inner surface generally smooth with two distinct finely granular central carinae and with upper border densely fringed with hairs; under surface with 26–31 fine striae; outer surface dorsally with fine dense granules tending to squamiform arrangement, with below two distinct finely granular carinae. Moveable finger—upper surface bearing three coarsely granular carinae; inner surface with almost smooth carinae below dense fringe of hairs; outer surface with finely granular carinae. Immovable finger—inner surface with two distinct finely granular carinae and two scattered rows of hairs; outer surface with two distinct almost smooth carinae. Both fingers—moderately robust, with sharp tips and blunt teeth.

Walking legs: Males with first leg modified—dactyl triradiate in section, distal part of merus with conspicuous raised collar. First leg: propodus with granular carina on outer border; carpus with two granular carinae on outer border. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with granular carina on outer border; carpus with two granular carinae on outer border and short, smooth carina near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus with finely granular carina on outer border; carpus with very finely granular carina on outer border and distally a rounded ridge near outer surface.

Fifth leg: Carpus with sharp hirsute anterior border; merus broad (L/B 1.95).

Merus of third maxilliped: Surface generally covered with moderately dense long hairs, sparser posteriorly, and without conspicuous granules; anterointernal angle produced; anteroexternal angle approximately a right angle; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment—broader than long, tip rounded, posterior border slightly curved, not deeply indented into penultimate segment; penultimate segment—broader than long, sides very slightly convex.

Male first pleopod: Evenly curving and tapering towards tip, without broad basal portion. Outer side—double row of long bipinnate hairs extending almost to tip, also bearing band of tubercles, terminating behind tip. Inner side—row of bipinnate hairs terminating some distance behind tip and scattered row of microscopic spinules beginning where bipinnate hairs finish and terminating behind tip.

Colour

(a) *Alcohol-preserved material:* After prolonged preservation reddish pigment on: carapace—borders of frontal and near tips of anterolateral teeth, small spots over almost entire carapace apart from gastric region, metagastric area with transverse patch only slightly longer than broad; chelipeds—distal portions of upper and inner surfaces of arm, boss on arm at wrist articulation, some granules on upper surface of wrist, granules on two innermost carinae of upper surface of hand, tubercles on hand at wrist and outer finger articulations, general inner surface of hand, granules on proximal two-thirds of upper surface of movable finger, inner and outer surface of base of proximal tooth of movable finger.

(b) *Dried material:* A male at the Smithsonian Institution (USNM 54632) without chelae shows the same pattern as the alcohol-preserved material.

(c) *Fresh material:* Dana (1852, p. 292) describes the colour of his material as follows: "Colour purple, in fine close dottings over the surface, becoming deep purple along the posterior of the median region which is convex posteriorly and sublunate in outline; posterior to this for some distance yellowish and also yellowish near the anterolateral margin. Carpus reticulate with purple above. Other legs in part purple or reddish purple, tarsus of last pair having a middle of pale blue, a narrow border of purple, and the marginal hairs yellow and penult joint similar". Presumably fresh material is described by Barnard (1950, p. 151) as follows: "Creamy-grey or pale buff, speckled with reddish dots, a median crescentic red mark and an oval red spot near each postero-lateral corner, hands of chelipeds tinged with red or pink inside surface (K.H.B.)". This is essentially repeated by Crosnier (1962), in French.

Distribution

S. Atlantic, Southern Indian Ocean, both coasts of S. America, but not from Australasia.

Remarks

In its pigmentation this species is closest to *O. punctatus* but shows no trace of anterior branchial pigment concentrations, and the posterior branchial blotches remain after prolonged preservation.

It is characterized by the fine, almost even, granulation of the carapace, and the fine dense granules on the outer dorsal surface of the hand of the cheliped, which tend to a squamiform arrangement. It shares with *O. elongatus* relatively fine and numerous striae on the under surface of the hand of the cheliped.

Ovalipes catharus (White)

Pls 36A, 38E, 38F, 42C; figs 1C, 2C, 3C, 4C

Portunus catharus White, in White and Doubleday, 1843, p. 265.

Platyonichus bipustulatus Miers, 1874, p. 2; pl. 1, fig. 1 (figure of type); 1876, p. 32. Hector, 1877, p. 473. Filhol, 1885, p. 383.

non *Platyonichus bipustulatus* H. Milne Edwards, 1834, p. 437 = *O. trimaculatus* (de Haan).

Ovalipes bipustulatus Chilton, 1911a, p. 292. Thomson, 1913, p. 237. Chilton and Bennett, 1929, pp. 755–7. Powell, 1949, p. 38, fig. 187. Richardson, 1949, p. 31 (key), figs 2, 2a. Dell, 1960, p. 5.

Ovalipes cf. *punctatus* Glaessner, 1960, p. 22; pl. 3, fig. 8 (Pleistocene fossil).

non *Corystes* (*Anisopus*) *punctata* de Haan, 1833, p. 44.

Ovalipes punctatus Dell, 1963, p. 43, text fig. Bennett, 1964, p. 64.

Notes on Synonymy

When it was realized that colour patterns might have diagnostic importance, data upon these patterns in New Zealand records of *Ovalipes* spp. were sought, and both material and photographs of material were obtained through the kind offices of Dr John C. Yaldwyn. As a result it was concluded that White's description (1843, p. 265) applied to this material on the basis of the colour being: ". . . carapace is brownish yellow, spotted with minute brown dots; the dots forming a lunated line between the impressions on back the most distinct. . ."

Evidently there are colour changes between live specimens, those recently preserved, and those kept for a period either wet or dry. On the basis of these variable artefacts Miers' (1874) and Powell's (1949) records belong to the present species. Hector's (1877) reference is included because he refers to Miers' recordings.

If there is only a single species of *Ovalipes* in New Zealand, as the present records indicate, the records of Thomson (1913), Chilton and Bennett (1929), and Richardson (1949) also belong to this species.

Some of Chilton's (1911a) Chatham Is. material has been examined and it belongs to the present species.

Material examined:—

Australia: Victoria: ♂ (89 mm), Beaumaris, pres. S. W. Fulton, May, 1902, NM.

South Australia: ♂ (66.5 mm), from Henry Edwards (old collection, dried), NM.

New Zealand: North Island: The following four specimens were all collected off Day's Bay, Wellington Harbour, 5/x/1953; ♀ (54 mm), AM P 14161; ♂ (54 mm), AM P 14162; ♀ (72 mm*), AM P 14163; ♂ (40 mm), AM P 14164. ♂ (72 mm), Wellington, NM, ex Colonial Museum of New Zealand. ♂ (68 mm), Point Howard,

Wellington, R. A. Falla, 10/viii/1963, DMNZ. 4 ♂♂ (damaged or fragmented), (c. 29–c. 54 mm), 4 ♀♀ (2 damaged), (c. 42–52 mm), Paraparaumu, M. Crozier, 13/iii/1965, drag net, DMNZ.

New Zealand (sic): ♀ (50 mm), Geodeffroy Collection, NM.

Chatham Is.: 3 ♂♂ (61–91 mm), 4 ♀♀ (63–101 mm), ♀ (ovig.) (86 mm), Chatham Is., "Nora Niven", N.Z. Govt. Trawling Exped., CM, ident. by Chilton and Bennett, 1927, as *Ovalipes bipustulatus* M. Edw.

Material illustrated: ♂ (72 mm) see * above.

Description:—

Front: Four-toothed (including inner supraorbital lobes); median teeth close together, fairly sharp, broadly separated from laterals and produced slightly further forwards than laterals; median fissure shallow; lateral teeth fairly sharp; subsidiary lateral lobe on lower plane than lateral tooth, relatively small, hirsute, with line of granules, and visible dorsally on inner side of lateral tooth.

Orbit: Upper border toothed, inner supraorbital notch deep; outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: With small flattened dorsal area, clearly visible dorsally, upper surface sparsely hirsute.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five; distinctly large and robust; broad based and narrowly separated, bordered by coarse granules; first tooth blunter than second, stout and truncate with broad base; fourth the largest; fifth the smallest and sharpest.

Carapace: Broad (B/L 1.37); areas generally not distinct, although with distinct but shallow cervical grooves; granulation fine throughout, but slightly coarser anteriorly; pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, subequal. Arm—anterior border without spines or tubercles; anterodistal border with large boss; posterior border coarsely and densely granular and distinctly hairy; under surface finely granular tending squamiform. Wrist—with long, robust inner spine; upper surface with spiniform tubercle at hand articulation, covered with fine and coarse granules, and with one distinct carina and traces of a second; outer surface with distinct carina bearing spiniform granules. Hand—not swollen, upper surface with boss at wrist articulation and with three distinct carinae, the innermost ending in a spine, between carinae very finely granular; inner surface with a few scattered small granules, with two distinct finely granular central carinae and with upper border densely fringed with hairs; under surface with 20–26 striae; outer surface with finely granular squamiform markings, with two distinct granular carinae. Movable finger—upper surface bearing three sharply granular carinae; inner surface with almost smooth carina below dense fringe of hairs; outer surface with finely granular carina. Immovable finger—inner surface with two distinct finely granular carinae and two scattered rows of hairs; outer surface with two distinct finely granular carinae. Both fingers—moderately robust, with sharp tips and blunt teeth.

Walking legs: Males with first leg modified—dactyl triradiate in section, distal part of merus with conspicuous raised collar. First leg: propodus with granular carina on outer border; carpus with two granular carinae on outer border. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with partly granular

carina on outer border; carpus with two granular carinae on outer border and short, granular ridge near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus with carina on outer border, proximally granular becoming more finely granular distally; carpus with partly granular carina on outer border and distally a short, rounded ridge near outer surface.

Fifth leg: Carpus with sharp, hirsute anterior border; merus broad (B/L 1.80).

Merus of third maxilliped: Surface generally partly covered with patches of hairs, sparser posteriorly; anterointernal angle rounded and bulging; anteroexternal angle very obtuse; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment—broader than long, tip relatively pointed, posterior border almost straight and deeply indented into penultimate segment; penultimate segment—as broad as long, with distinctly convex sides.

Male first pleopod: Evenly curving and tapering towards tip, without broad basal portion. Outer side—double row of bipinnate hairs extending about two-thirds length of appendage, also bearing a broad band of tubercles extending almost to tip. Inner side—double row of bipinnate hairs terminating some distance behind tip, and band of microscopic spinules beginning where bipinnate hairs finish and terminating behind tip.

Colour

(a) *Alcohol-preserved material:* After a relatively short preservation, reddish pigment on: carapace—fairly dense border to entire carapace, particularly frontal and anterolateral teeth, small spots evenly and fairly densely distributed apart from lighter areas in gastric region and postlateral junction, and apart from distinct concentrations in each anterior branchial region; V-shaped metagastric mark, and distinct but relatively small blotches in posterior branchial region; chelipeds—general upper surface with concentrations on boss of arm at wrist articulation, proximal three-quarters of inner surface of movable finger, and dorsal proximal area of inner surface of movable finger.

The colour of this species evidently changes after preservation. Powell (1949) describes the colour as: "The general colouring is speckled bluish to sandy grey with two violet-coloured blotches near the bottom of the carapace." Dr John C. Yaldwyn (personal communication) confirms the two coloured blotches. Powell's (1949) figure (187) shows very indistinct postlateral blotches, and a slight concentration of colour in the gastric region.

As indicated above, after keeping for a relatively short while in alcohol, there are five main pigmented areas, with a conspicuous "butterfly mark" in the gastric region.

White's (1847) description mentions minute brown dots, concentrated in a "lunated line between the impressions on back", and evidently refers to the butterfly mark. This is clearly seen in another photograph from the Dominion Museum, New Zealand, in which, apart from this concentration, only traces remain of anterolateral and posterolateral pigment concentrations. Data on this specimen are: old, dried specimen, Wellington, N.Z., negative B. 4646.

Miers' (1874) plate of White's type shows only general speckling, and evidently the central mark had also faded in the interim.

(b) *Fresh material* (taken from a colour transparency of a fresh specimen, through the courtesy of Dr J. C. Yaldwyn, Australian Museum, Sydney). Data on the specimen from the Dominion Museum, Wellington are: ♂, Day's Bay, Wellington, R. A. Falla, May, 1959, DMNZ Cr. 853. Carapace—basically yellowish-brown,

with conspicuous white patches in the postlateral regions; generally overlaid with blackish purple pigment as follows: small, dense spots covering carapace except in white postlateral regions and white H-shaped cervical grooves; dense concentration along borders of anterior half of carapace; a small, but conspicuous, round patch in each anterior branchial region; dense butterfly-shaped mark in cervical grooves just anterior to white area; a large conspicuous oval patch in each postlateral region on median edge of white area. Chelipeds—generally reddish-orange on upper and inner surfaces with concentrations of blackish-purple on: distal inner border of arm; base of inner spine of wrist; upper, inner carina of hand. Under surfaces of chelipeds and tips of fingers white. Dell's (1963) figure shows markings identical to those of the above specimen.

Distribution

Previously known only from New Zealand and the Chatham Is. The present records are the only ones from Australia.

Remarks

In its pigmentation after recent preservation this species is close to *O. punctatus* but differs in having usually finer and more numerous striae on the under surface of the hand of the cheliped, and in having finely granular carinae on the upper surface of the hand.

In the Chatham Is. specimens, the carapace granulation tends to be finer than in New Zealand mainland material, but with overlap. In addition, the third maxillipeds tend to be more hirsute.

The cheliped fragment of a New Zealand Pleistocene fossil shown in Glaessner (1960, pl. 3, fig. 8) is much closer to *O. catharus* than any other species of the genus and, as far as can be judged from his plate, belongs to this species. On the other hand, his *Ovalipes* sp. a (p. 23, pl. 3, fig. 9) is clearly not *O. catharus*. It does not appear to belong to any of the known present-day species, but has resemblances to both *O. punctatus* and *O. australiensis*.

Ovalipes australiensis n. sp.

Pls 35C, 35D, 39A, 39B, 41F, 41G, 42D; figs 1D, 2D, 3D, 4D

Platyonychus bipustulatus Haswell, 1882, pp. 84–5. Miers, 1886, p. 202.

non *Platyonichus bipustulatus* H. Milne Edwards, 1834, p. 437.

Platyonychus bipustulosus Whitelegge, 1900, p. 158.

Ovailipes trimaculatus Fulton and Grant, 1906, p. 18.

non *Corystes* (*Anisopus*) *trimaculata* de Haan, 1833, p. 13.

Ovalipes bipustulatus Hale, 1927, pp. 147–8, fig. 148.

Ovalipes punctatus Stephenson and Campbell, 1960, pp. 89–90, figs 1C, 2E; pl. 2, fig. 2; pl. 5E (excluding Lord Howe Is. specimens). McNeill, 1962, pp. 38 (plate), 41; 1964, pp. 2 (plate), 4–5.

non *Corystes* (*Anisopus*) *punctata* de Haan, 1833, p. 44.

Holotype: ♂ (97 mm), Lake Illawarra, New South Wales, pres. G. McAndrew before 1923, AM P 6265.

Material examined:—

Pacific Ocean: ♂ (51 mm), Pacific Ocean, MM.

Australia. Queensland: ♀ (38 mm), Wide Bay, AM P 15409 (Haswell collection). ♂ (24 mm), Southport, coll. R. Pohlman, QM W 2376. ♀ (38 mm), Point Lookout,

Stradbroke I., coll. W.S., 27/v/1953, fishing line, ocean sand beach, QM W 2377. ♀ (51 mm), Miami Beach, South Coast, coll. B. Winks, 22/viii/1953, low tide but still receding, swimming and burrowing, AM P 13468. 40 ♂♂ (26–97 mm), 19 ♀♀ (35–74 mm), trawled in shallow water off Southport, "Irene June", J. Laurence, 24/xi/1964, QM W 2669—W 2673. 50 ♂♂ (31–76 mm), 53 ♀♀ (32–63 mm), trawled in shallow water between Southport and Jumpin Pin Bar, "Irene June", J. Laurence, 16/xii/1964, QM W 2664—W 2668.

New South Wales: ♂ (98 mm), Port Jackson, QM W 2378. ♂ (55 mm), ♀ (56 mm), Port Jackson, USNM 17031, ident. M. J. Rathbun as *Platyonychus bipustulatus* then as *Ovalipes punctatus*. 2 ? sex (18.8, ? mm), Port Jackson, AM P 15410 (Haswell collection). ♀ (78 mm), Port Jackson, AM P 15407 (Haswell collection). 2 ? ♀♀ (14, 18 mm), Port Jackson, AM P 15408 (Haswell collection). 2 ♂♂ (18, 55 mm), Port Jackson, MM. 2 ♂♂ (60, 69 mm), ♀ (66 mm), Port Jackson, MM. ♂ (22 mm), Port Stephens, MM. 3 ? sex (29–31 mm), Port Stephens, MM. Juv. (damaged, c. 17 mm), Jervis Bay, T. Whitelegge, Oct. 1893, AM G 904. ♂ (39 mm), ovig. ♀ (69 mm), Newcastle Bight, coll. E. R. Waite, 1898, "Thetis" Sta. 23, 19–16 fm, AM G 2358. ♀ (58 mm), New South Wales, purchased Mrs F. E. Grant, Feb., 1907, AM G 5869. 2 ♂♂ (26, 54 mm), Port Jackson, Mar., 1908, AM P 225 (old collection). ♂ (74 mm), Broken Bay, Apr., 1908, AM P 316 (old collection). ♀ (67 mm), Broken Bay, Apr., 1908, AM P 317 (old collection). ♀ (24 mm), Port Jackson, Oct., 1908, AM P 1192 (old collection). ♂ (84 mm), AM P 3620; ♂ (68 mm), AM P 3621; ♂ (70 mm), AM P 3622; ♀ (47 mm), AM P 3623; ♀ (55 mm), AM P 3624; all La Perouse, Botany Bay, pres. R. J. Thorpe, Mar., 1913. ♂ (57 mm), Nelson's Bay, Port Stephens, exch. E. A. Briggs, Sydney University, Aug., 1920, AM P 4872. ♀ (59 mm), AM P 6536; ♀ (59 mm), AM P 6537; ♀ (53 mm), AM P 6583; ♂ (52 mm), AM P 6539 (third anterolateral tooth on right side, divided into two); ♀ (70 mm) AM P 6540; all Maroubra Bay, coll. F. A. McNeill and party, 1/ii/1923. ♀ (soft), (35 mm), Coogee Beach, pres. G. P. Whitley, 12/ii/1924, washed up, AM P 7080. ♀ (25 mm), beach at The Basin, Pittwater, Broken Bay, pres. H. O. Fletcher and party, Mar., 1924, AM P 7124. Juv. (18 mm), North Harbour, Manly, coll. J. R. Kinghorn and T. Campbell, 13/x/1924, burrowing in sand, AM P 7568. ♂ (33 mm), Gunnamatta Bay, Port Hacking, Oct., 1925, tidal flat, USNM G 4679, prev. ident. as *Ovalipes punctatus*. ♀ (55 mm), Ocean Beach, South West Rocks near Kempsey, pres. M. Ward, Nov., 1925, USNM 76539, ident. by M. Ward as *Ovalipes punctatus*. 4 ♂♂ (13–19 mm), ♀ (18 mm), dredged Sow and Pigs Reef, Port Jackson, 26/x/1926, c. 3 fm., sandy mud, USNM 64558. 5 juvs. (13–14 mm), off Balmoral, Port Jackson, coll. F. A. McNeill and party, Nov., 1926, c. 3 fm., AM P 8724. ♂ (28 mm), Gunnamatta Bay, Port Hacking, coll. F. A. McNeill and party, Mar., 1929, AM P 9338. ♂ (36 mm), AM P 12677; ♀ (13 mm), ovig. ♀ (27 mm), AM P 12678, near mouth Shoalhaven R., pres. CSIRO Fish. Div., 2/xi/1938, Agassiz trawl. ♂ (79 mm), Green Pt, Yamba, mouth Clarence R., pres. A. A. Cameron, 25/xii/1939, washed up, AM P 11253. 4 ♂♂ (34–41 mm), Lake Macquarie, coll. CSIRO Fish. Div., 1953, AM. ♀ (42 mm), Kurnell Peninsula, S. Sydney, coll. A. J. Coventry, 20/iv/1956, NM. ♀ (79 mm), Cronulla beach, coll. I. G. Filmer, 8/iv/1957, QM W 1978. Six dried carapaces, Arrawarra Sta. Univ. New England, 23/x/1965, strand line, coll. W. S. and M. R. (not kept).

Victoria: ♀ (35 mm), Port Phillip, pres. J. Bracebridge Wilson, Aug., 1892, AM G 623. 2 ♂♂ (24.5, 47 mm), on reef at Point Lonsdale, Feb., 1903, NM. 2 ♂♂ (c. 62, 76 mm), Queenscliffe, Melbourne, coll. Edgar L. White, Nov., 1905, AM G 5457. ♂ (60 mm), Port Phillip. ex. M. Ward, Sept., 1924, plentiful on sand flats in shallow water, AM P 7487. ♂ (69 mm), "taken out of bottle containing Victorian fish, no label attached", NM, ident. by M. Ward, 1929 as *Ovalipes bipistulatus* (sic). ♂ (61

mm), ♀ (67 mm), off Fisherman's Bend, Hobson Bay, II Aquarium, 2/v/1932, NM. ♂ (55.5 mm), Portsea, coll. O. White 5/iii/1936, NM. ♀ (33 mm), 44782; ♀ (63 mm), 44783; ♂ (64.5 mm), 44784; ♂ (108.5 mm), 44785; ♀ (69 mm); all Brighton, collections undated, NM.

Tasmania: ♂ (soft and fragmented), (c. 76 mm), Cowrie Pt, Brickmakers Bay, Stanley, coll. B. M. Wragg, Jan., 1948, QVM 1957-10-18. ♂ (38 mm), Seven Mile Beach, Frederick Henry Bay, coll. V. V. Hickman, 29/xii/1955, AM P 13466. 2 ♂♂ (42, 50 mm), 4 ♀♀ (49–57 mm), Waterhouse I., N.E Tasmania, coll. R. H. Green, 17/viii/1962, netted on beach at night, QVM 1965-10-2, previously ident. by R. H. G. as *Ovalipes bipustulatus*.

South Australia: ♂ (49 mm), 40 miles E. of Kingston, Kangaroo I., pres. Comm. Fish. Bureau, Sept., 1909, 30 fm., AM P 2303. ♂ (88 mm), Pt Willunga, coll. H. M. Hale, approx. 1926, S Aust M C 1203, previously ident. as *Ovalipes bipustulatus* M. Edw. presumably by H. M. Hale. ♂ (69 mm), ♀ (39 mm) St Vincent Gulf, coll. H. M. Hale, approx. 1926, S Aust M C 1204, previously ident. as *Ovalipes bipustulatus* presumably by H. M. Hale. ♂ (50 mm), West of Kingston, "Endeavour", WAM 39–60. ♂ (43 mm), mouth of Murray R., "Endeavour", 17/viii/1909, 20 fm., QM W 1530. 6 ♂♂ (41–71 mm), ovig. ♀ (70 mm), Gt Australian Bight, 36° 00′ S., 138° 21′ E., 6/xii/1951, ST 300 on sand, 64 metres "Galathea" Sta. 563, UZM. 16 ♂♂ (44–75 mm), 6 ♀♀ (44–71 mm), ovig. ♀ (59 mm), Gt Australian Bight, 36° 18′ S., 138° 29′ E., 6/xii/1951, HOT and ST 600, on sand, 60 m, "Galathea" Sta. 564, UZM. ♂ (31 mm), from W. Kershaw, NM. ♂ (69.5 mm), from Henry Edwards, old collection, NM.

Western Australia: ♂ (66 mm), Carnac I., Fremantle, pres. J. M. Sheridan, May, 1905, AM G 5307. 2 ♂♂ (74, 79 mm), Garden I., W. B. Alexander and Justin Burnside, Jan., 1914, WAM 90–12. ♂ (81 mm)*, Cottesloe, L. Glauert, Dec., 1923, WAM 107–42. ♂ (71 mm), Albany, H. McKail, Mar., 1931, WAM 354–31. ♀ (25 mm), 10 miles E. of Hopetown, R. W. George, 10/i/1959, WAM 45–63. ♀ (61 mm), Esperance Bay, W. H. Butler, 20/ii/1959, jetty piles, WAM 47–63. 2 ♀♀ (70, 72 mm), Bunker Bay near Cape Naturaliste, R. W. George, 9/iii/1959, caught on on fishing line from beach, WAM 40–63. ♂ (56 mm), Torbay, B. K. Bowen, on "Bluefin", 9–13/vi/1959, 20–25 fm., in craypot, fish bait, rock bottom, WAM 48–63. ♀ (45 mm), Esperance, W. H. Butler, Mar., 1960, WAM 43–63. ♀ (29 mm), 2 miles W.NW. of Cottesloe, near buoy, 4 fm., R. W. George on "Davena", 5/v/1960, WAM 42–63. 2 ♂♂ (54, 85 mm), off Cottesloe in prawn trawl, D. Wright on "Peron", 20/vii/1961, WAM 38–63. ♀ (84 mm)‡, North Point, Rottnest I., J. Seabrook on "Lancelin", 25/x/1961, caught on beach, WAM 41–63. ♂ (33 mm), juv. (15 mm), Dunsborough, Barry Wilson, 25/xii/1961, dredged 2 fm., WAM 44–63. 2 ♀♀ (80, 89 mm), just inside bar, Mandurah Estuary, Mrs D. George, 12/vi/1962, in crab dragnet, WAM 39–63. 2 ♀♀ (both 45 mm), approx. 7 miles W. of City Beach, Perth, R. W. George, 15/viii/1962, trawled 16 fm, WAM 46–63.

Material illustrated: ♂ (81 mm), WAM 107–42, see * above (line drawings, photographs of chelipeds and first walking leg), ♀ (84 mm), WAM 41–63 (see ‡ above) (dorsal view photograph).

Description:—

Front: Four toothed (including inner supraorbital lobes); median teeth close together, broadly separate from, and produced further forward than laterals; median fissure shallow; all teeth fairly sharp; subsidiary lateral lobe on lower plane than lateral tooth, relatively large, very hirsute, with few granules and visible dorsally on inner side of lateral tooth.

Orbit: Upper border toothed; inner supraorbital notch deep; outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: Without flattened dorsal area; largely obscured dorsally by hirsute frontal border, upper surface with long dense hairs.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five; distinctly large and robust; broad based and narrowly separated, bordered by coarse granules; first tooth slightly blunter than second and with broad base, sharp tip, somewhat truncate; fourth the largest; fifth the smallest and sharpest.

Carapace: Broad (B/L 1.37); areas not generally distinct although with distinct cervical grooves; anterior granulation coarse; posterior granulation fine; pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, subequal. Arm—anterior border without spines or tubercles; anterodistal border with large boss; posterior border coarsely and densely granular and distinctly hairy; under surface finely granular, tending squamiform. Wrist—with long robust inner spine; upper surface with small sharp tubercle at hand articulation, covered with fairly dense coarse granules, without carinae; outer surface moderately finely granular and without carina. Hand—slightly swollen, upper surface with boss at wrist articulation, with three distinct carinae the innermost ending in a sharp spine, between carinae coarsely granular; inner surface with coarse scattered granules, with two distinct coarsely granular central carinae and with upper border densely fringed with hairs; under surface with 17–24 moderately coarse striae; outer surface generally coarsely granular, with two distinct carinae, the dorsal coarsely granular, the ventral moderately finely granular. Movable finger—upper surface bearing three carinae of spiniform granules; inner surface with finely granular carina below dense fringe of hairs, lower border with scattered row of hairs; outer surface with moderately finely granular carina. Immovable finger—inner surface with two granular carinae and two rows of hairs, dense proximally, scattered distally; outer surface with two distinct granular carinae. Both fingers—robust with fairly sharp tints and blunt teeth.

Walking legs: Males with first leg modified—dactyl triradiate in section, distal part of merus with conspicuous raised collar. First leg: propodus with granular carina on outer border; carpus with two granular carinae on outer border. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with partly granular carina on outer border; carpus with two granular carinae on outer border and short, partly granular ridge near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus with carina on outer border; carpus with partly granular carina on outer border and distally a short, rounded, partly granular ridge near outer surface.

Fifth leg: Carpus with sharp, hirsute anterior border; merus broad (L/B 1.77).

Merus of third maxilliped: Surface generally covered with moderately long hairs, dense anteriorly, sparse posteriorly, without conspicuous granules, and with a distinct oblique row of hairs; anterointernal angle slightly produced; anteroexternal angle almost a right angle; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment—as broad as long, tip narrow but rounded, posterior border curved, not deeply indented into penultimate segment, sides concave. Penultimate segment—slightly broader than long.

Male first pleopod: Evenly curving and tapering towards tip, without broad basal portion. Outer side—dense double row of bipinnate hairs on proximal two-thirds terminating behind tip, also bearing band of tubercles terminating almost at tip. Inner side—dense row of bipinnate hairs apart from near tip, row of microscopic spinules present beginning within the row of hairs and terminating behind tip.

Colour

(a) *Alcohol-preserved material:* After prolonged preservation when reddish pigment is visible it is distributed as follows: carapace—borders of frontal teeth, just behind tips of anterolateral teeth, each posterior branchial area with discreet rounded oval patch; chelipeds—general upper surface and anterodistal portion of inner surface of arm, surrounding but not on boss on arm at wrist articulation, general upper and inner surfaces of wrist, granules on upper surface of hand, tubercle on hand at wrist articulation, dorsal half of inner surface of hand, granules on upper surface of movable finger, proximal two-thirds of inner surface of movable finger, and proximal half of dorsal portion of inner surface of immovable finger.

(b) *Fresh material:* (As noted by the authors.) Carapace—generally covered with small red dots, concentrated to form pigment lines behind orbits, and pigmented spots on tips of frontal and first four anterolateral teeth. Pigment absent from a narrow H-shaped area in region of cervical grooves and from a number of small circular areas marking anterior border of branchial region. Each posterior branchial region with a dense, discrete, oval, blood-red mark (Hale, 1927, describes these marks as violet and Dakin, 1952, as "blood-red to mauvish"). On wrist and inner surface of hand of cheliped pigment forms a squamiform pattern.

Juveniles (*pl.* 35*D*)—Identification of the following specimens caused initial difficulty: *South Australia*, 2 juvs (dried), (both c. 7 mm), St Vincent Gulf, coll. H. M. Hale, approx. 1926, S Aust M C 1203, previously ident. as *Ovalipes bipustulatus* M. Edw., presumably by H. M. Hale.

These specimens differ from large *O. australiensis* in: (1) median frontal teeth protruding well forwards; (2) all frontal teeth blunt; (3) subsidiary lateral frontal teeth not visible on inner side of lateral teeth; (4) inner supraorbital notch absent; (5) anterolateral teeth all narrow and sharp pointed, fourth tooth not distinctly larger than third; (6) carapace elongate (B/L 1.15, 1.12); (7) carapace areas very distinct; (8) granulations in central regions of carapace coarser than in lateral regions; (9) undersurface of palm of cheliped with 25 striae; (10) merus of fifth leg elongate (L/B 2.45–2.66); and (11) third maxilliped with more obtuse anteroexternal angle and with convex inner anterolateral border.

Three slightly larger dried specimens in the collections of the National Museum of Victoria (24.5 mm male, Point Lonsdale, Victoria; 33 mm female, Brighton, Victoria, No. 44782; and 31 mm male, S. Australia from W. Kershaw) are intermediate in their morphological features and link the above juveniles to the bulk of the collection.

Distribution

This species has only been recorded from the southern half of Australia ranging from Wide Bay, Queensland to Cape Naturaliste, Shark Bay, Western Australia. It has been extremely common near the northern known limit of its distribution on the eastern Australian coast. One specimen has been recorded from Lord Howe I. on the basis of a colour photograph seen by the authors.

Remarks

The pigmentation of fresh specimens is unique, with two discrete postlateral oval areas, but without trace of a metagastric pigmented area. It is also characterized by distinctly coarse granulation on the anterior surface of the carapace, and by the coarse granulation of the general upper surface of the chelipeds (excluding carinae).

Ovalipes elongatus n. sp.

Pls 36B, 39C, 39D, 42E; fig. 1E

Ovalipes bipustulatus Chilton, 1911 b, p. 554.

non *Platyonichus bipustulatus* H. Milne Edwards, 1834, p. 437.

Holotype: Lord Howe I.: ♀ (33 mm), Blinkenthorpe Beach, May, 1964, rock, Isobel Bennett, AM P 15387.

Material examined. Paratypes as follows:

Lord Howe I.: (Tasman Sea) Juv. ♀ (18 mm), Oct., 1908, on reef, pres. A. R. McCulloch, AM P 1132. ♀ (38 mm), rec'd 6/vii/1915, coll. R. S. Bell, W. R. B. Oliver collection, DMNZ. ♀ (38 mm), (dried), Feb., 1938, pres. Dr Sweet, AM P 10936. ? ♀ (24.5 mm), Lagoon Beach, Sept., 1966, washed up on beach, Mrs F. Evans, AM P 15182. Carapace only (C. 27.5 mm), Lagoon Beach, Sept., 1966, washed up on beach, Mrs F. Evans, AM P 15183.

Kermadec Is.: (N. of New Zealand) ♀ (28 mm), 2 juvs. (both 13 mm), 1908, W. R. B. Oliver, CM, prev. ident. by C. Chilton as *Ovalipes bipustulatus*.

Material illustrated: Holotype.

Description:—

Front: Four toothed (including inner supraorbital lobes), median teeth close together, moderately sharp, broadly separated from laterals, and produced slightly further forwards than laterals; median fissure shallow; lateral teeth sharp; subsidiary lateral lobe on lower plane than lateral tooth, relatively large, sparsely hirsute, with line of granules, and visible dorsally on inner side of lateral tooth.

Orbit: Upper border toothed; inner supraorbital notch deep; outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: With small flattened dorsal area; clearly visible dorsally; upper surface sparsely hirsute.

Basal joint of second antenna: With flattened dorsal area, visible in larger specimens only when antenna moved dorsally.

Anterolateral teeth: Five; distinctly large and robust; broad based and narrowly separated; bordered by moderately coarse granules; first tooth blunter than second and sharp with broad base; fourth the largest; fifth the smallest and sharpest.

Carapace: Relatively elongate (B/L 1.19–1.25); areas generally not distinct, although with distinct cervical grooves; granulation fairly coarse anteriorly, fine posteriorly; pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, subequal. Arm—anterior border without spines or tubercles; anterodistal border with large boss; posterior border granular and variably hirsute (varying from sparsely to densely hirsute); under surface finely granular tending squamiform. Wrist—with long, robust inner spine; upper surface covered with fine, moderately dense granules and traces of one carina; outer surface with indistinct, finely granular carina. Hand—swollen, upper surface with boss at wrist articulation and with three distinct carinae, the innermost ending in a spine, between carinae finely or microscopically granular; inner surface generally smooth

with two indistinct finely granular carinae, and with upper border densely fringed with hairs; under surface with typically 23–27 (in the largest Kermadec Is. specimen, 20) moderately fine striae extending to under surface of immovable finger; outer surface dorsally with dense granules, with below two finely granular carinae, the lowermost very inconspicuous. Movable finger—upper surface bearing three granular carinae; inner surface with smooth carina below dense fringe of hairs; outer surface with carina varying from smooth to finely granular. Immovable finger—inner surface with two distinct, smooth carinae and two scattered rows of hairs; outer surface with two distinct almost smooth carinae. Both fingers—moderately robust, with sharp tips and blunt teeth.

Walking legs: First leg: dactyl with flattened grooved surfaces and carinate edges; propodus with smooth carina on outer border; carpus with two inconspicuous carinae on outer border. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with smooth carina on outer border; carpus with smooth carina on outer border and below this, a short smooth carina, distally a short, rounded ridge near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus with carina on outer border; carpus with carina on outer border and distally an inconspicuous short rounded ridge near outer surface.

Fifth leg: Carpus with sharp, hirsute anterior border; merus fairly broad (L/B 2.22 in larger specimens, 2.05 in juveniles).

Merus of third maxilliped: Surface generally covered with moderately dense long hairs, sparser posteriorly, without conspicuous granules; anterointernal angle produced; anteroexternal angle rounded; posterointernal surface with distinct raised edge.

Male abdomen and first pleopod: There are no adult males in the present collection.

Colour

(a) *Alcohol-preserved material:* After 1½ years preservation: reddish orange pigment on: carapace—bases of frontal and anterior bases of anterolateral teeth, distantly spaced sinuous lines over most of carapace, metagastric area with relatively thin crescent-shaped mark, no distinct patch on posterior branchial area but here one of the carapace lines is thickened (this not recognizable in Kermadec Is. specimens); chelipeds—small patch on distal upper surface of arm, boss at wrist articulation, broken sinuous lines on upper surface of wrist, granules on two innermost carinae of upper surface of hand, tubercle on hand at wrist articulation, transverse band near proximal end of upper surface of movable finger.

(b) *Dried material:* This differs from the above only in having fainter carapace markings apart from those in the posterior branchial area, where the thickened lines approximate to a band.

Distribution

Known only from Lord Howe I. and Kermadec Is.

Remarks

Chilton (1911b), p. 554 describes the colour of his Kermadec Is. material as: "... carapace is light grey almost lavender, and the joints of the arms bright red, tinging near the claws to dark orange". Bennett (1966, pl. 101(a)) has given photograph of the holotype which indicates the fresh colour pattern.

This species is characterized by its unique pigmentation and elongate carapace. It resembles *O. trimaculatus* in the fine and numerous striae on the under surface of the hand of the cheliped.

Ovalipes georgei n. sp.

Pls 36C, 39E, 39F, 40C, 42F; figs 1F, 2E, 3E, 4E

Holotype: West Australia: ♂ (46 mm), 5½ miles NW. off Rottnest I., P. Cawthorne on "Lancelin", 11/xi/1961, main light, in plankton net at surface, WAM 120–61.

Material examined: Paratype: ♂ (38 mm), just off Cottesloe, D. Wright on "Peron", 20/vii/1961, in prawn trawl, WAM 121–61.

Material illustrated: Holotype.

Description:—

Front: Four toothed (including inner supraorbital lobes); median teeth close together, moderately sharp, broadly separated from laterals, not produced further forwards than laterals; median fissure shallow; lateral teeth sharp; subsidiary lateral lobe directly below lateral tooth, bordered by hairs, granule on tip.

Orbit: Upper border toothed; inner supraorbital notch feebly developed; outer supraorbital notch present; suborbital border hairy.

Basal joint of first antenna: With flattened dorsal area.

Basal joint of second antenna: With flattened dorsal area.

Anterolateral teeth: Five, distinctly large and robust; fairly narrow based and narrowly separated, bordered by coarse granules; first tooth blunter than second, sharp with relatively narrow base; fourth tooth the largest; fifth the smallest and sharpest.

Carapace: Relatively elongate (B/L 1.20), areas distinct, covered by densely packed, conspicuous, tubercle-like granules except in the postlateral regions, where granules are fine. Protogastric region, with line of three inconspicuous granular elevations, mesogastric region with conspicuous almost spinous elevation. In each posterior branchial region a conspicuous granular ridge. Pterygostomial area diffusely granular.

Chelipeds: Relatively short, robust, left larger than right. Arm—anterior border without spines or tubercles; anterodistal border with large boss; posterior border coarsely and densely granular and distinctly hairy, under surface tending squamiform. Wrist—with long, very robust inner spine; upper surface without tubercle at hand articulation, covered with conspicuous granules, and without carinae; outer surface without carina. Hand—swollen, upper surface with boss at wrist articulation and with three distinct carinae, the innermost ending in a spine, between carinae coarsely granular; inner surface generally smooth, upper border densely fringed with hairs and on large cheliped, two distinct finely granular carinae; under surface tending squamiform and finely granular; outer surface coarsely granular, bearing two distinct granular carinae. Movable finger—upper surface bearing three almost spiniform granular carinae; inner surface with smooth carina below dense fringe of hairs, outer surface with finely granular carina. Immovable finger—inner surface with two microscopically granular carinae and two scattered rows of hairs; outer surface with two distinct finely granular carinae. Both fingers—robust, with sharp tips and blunt teeth.

Walking legs: Males with first leg modified—dactyl triradiate in section. First leg: propodus with smooth carina on outer border; carpus with two carinae on outer border, uppermost granular, lowermost smooth, line of granules near outer surface. Second leg: dactyl with flattened grooved surfaces and carinate edges; propodus with carina on outer border; carpus with smooth carina on outer border and below this a short smooth ridge, distally a line of granules near outer surface. Third leg: dactyl with flattened grooved surfaces and carinate edges; propodus and carpus with smooth carina on outer border.

Fifth leg: Carpus with strong, cornifield carina along anterior edge; merus broad (L/B 1.94), and with boss at posterodistal extremity.

Merus of third maxilliped: Anterior surface densely covered with long hairs, posterior surface almost naked; without conspicuous granules; anterointernal angle produced; anteroexternal angle rounded; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment broader than long, tip rounded, posterior border curved and indented into penultimate segment; penultimate segment broader than long, sides markedly convex.

Male first pleopod: Evenly curving and tapering towards tip, without broad basal portion. Outer side—sparse scattered row of bipinnate hairs ending some distance behind the tip, also bearing band of tubercles terminating behind tip. Inner side—row of bipinnate hairs becoming sparser distally, ending some distance behind tip, short row of microscopic spinules beginning within region of hairs and ending distinctly behind tip.

Colour

(a) *Alcohol-preserved material:* Carapace—greenish-grey ground colour on anterior half, fading to cream posteriorly; elevations on anterior half of carapace tinged with pink; chelipeds with red spot on boss of arm at wrist articulation; dactyl of fifth leg with pink suffusion distally.

(b) *Fresh material:* Shortly after collection the following notes were made on the holotype by Dr R. George: "Carapace pale grey anteriorly, fine orange spots posteriorly. Dactyl of fifth leg with blood red spot".

Remarks

This species possesses a unique stridulating apparatus involving movement of the modified fifth leg against the granular ridge in the posterior branchial area of the carapace. It is named after Dr Ray George, who sent the present specimens to us and also drew our attention to the probable existence of certain of the species previously synonymized under *O. punctatus*.

Ovalipes iridescens (Miers)

Pls 36D, 40A, 41A, 42G; figs 1G, 2F, 3F, 4F

Platyonychus iridescens Miers, 1886, p. 202; pl. 17, fig. 2.

Ovalipes iridescens (Miers). Yokoya, 1933, p. 174. Leene, 1938, p. 2. Sakai, 1939, pp. 376–5; pl. XLII, fig. 4; 1965, p. 112 (in generic synonymy). Grindley, 1961, pp. 129–30, figs 2a–d.

Material examined:—

South Africa: ♂ (112 mm), trawled off Lourenco Marques, S Afr M A 12123.

Indonesia. Banda Sea: 2 ♂♂ (46*, 50 mm), ♀ (47 mm), 5° 28′ 4″ S., 132° 0′ 2″ E., "Siboga" Sta. 251, depth 204 m, ZMA De. 102, 151.

Japan: ♀ (34 mm), ovig. ♀ (36 mm), Tosa Bay, S. Japan, 80–120 m, pres. Dr Sakai (forwarded to Australian Museum).

Australia. Victoria: ♂ (63 mm‡) juv. (16 mm), SSW. of Mt Cann, 40 miles, 27/viii/1914, 74 fm, AM P 15370–1 (in company with *O. molleri*).

Material illustrated: ♂ (46 mm), see * above (dorsal view photograph). ♂ (63 mm), see ‡ above (line drawings, photographs of chelipeds and pterygostomial region).

Description:—

Front: Three toothed (including inner supraorbital lobes); median tooth produced much further forwards than laterals; all teeth sharp; subsidiary lateral lobe on general frontal border relatively feebly developed.

Orbit: Upper border not toothed; supraorbital notch fairly deep; suborbital border sparsely hirsute.

Basal joint of first antenna: Protruding well forwards, with flattened dorsal area, carrying small hairs.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five; generally small and sharp; narrow based and broadly separated; between teeth bordered by fine granules; first tooth largest, blunter than second; second tooth smallest.

Carapace: Moderately broad (B/L 1.28); areas generally distinct, without tubercular elevations and with two almost oval areas of very thin cuticle in posterior half; general granulation moderately fine throughout, but smooth in the two areas of thin cuticle, in indented areas posterolateral to them, and in central cardiac area; pterygostomial area with conspicuous but narrow striated ridge terminating medially in a granular patch.

Chelipeds: Relatively long, thin, subequal. Arm—anterior border proximally very finely granular, distally with 2–5 sharp spines; anterodistal border with large boss; posterior border sparsely and finely granular and without hairs; under surface finely to coarsely granular, tending squamiform in larger specimens. Wrist—with moderately robust inner spine, sharp in smaller specimens; upper surface with sharp, well-developed spine at hand articulation and two granular carinae, general upper surface finely and sparsely granular; outer surface with one indistinct granular carina terminating in a well-developed spine. Hand—slightly swollen; upper surface with distinct boss at wrist articulation, with three granular carinae, outermost very well-developed and separating upper and outer surfaces, central one distinct, innermost distally bearing four spines, between outer and central carina very sparsely granular, between central and inner, granular; inner surface with upper border fringed with hairs, with two inconspicuous central, very finely granular carinae and conspicuous lower carina moderately coarsely granular; under surface granular tending squamiform; outer surface dorsally sparsely granular, central granular carina, ventrally granules in squamiform pattern. Movable finger—upper surface outer margin bearing densely, moderately coarsely, granular carina, inner margin bearing 4–5 sharp well-developed spines increasing in size distally, between margins smooth; inner surface on upper border moderately dense fringe of hairs, below this general surface finely granular; outer surface very finely granular. Immovable finger—inner surface with two inconspicuous finely granular carinae, outer surface finely granular with one pitted groove. Both fingers—relatively long and slender with sharp tips and moderately blunt teeth.

Walking legs: First leg: dactyl very long, sharp, with slightly flattened, grooved surfaces and carinate edges; propodus with smooth carina on outer border and smooth ridge near outer surface; carpus with two smooth ridges on outer border, lowermost inconspicuous. Second leg: dactyl strongly carinate, almost quadradiate in section; propodus with smooth carina on outer border and smooth ridge near outer surface; carpus with smooth carina on outer border. Third leg: dactyl strongly carinate, almost quadradiate in section; propodus with partly granular carina on outer border; carpus with smooth carina on outer border.

Fifth leg: Carpus with carina on anterior border projecting slightly at distal end; merus moderately broad (L/B 2.17).

Merus of third maxilliped: Surface anteriorly hairy, posteriorly almost smooth; anterointernal angle slightly produced; anteroexternal angle very obtuse and barely recognizable as an angle; posterointernal surface without distinct raised edge.

Male abdomen: Ultimate segment much broader than long, tip rounded, narrower proximally than in centre and with sharply convex sides, posterior border straight, deeply indented into penultimate segment; penultimate segment slightly longer than broad.

Male first pleopod: Proximal half very broad then narrowing abruptly and tapering to tip. Outer side—bearing bipinnate hairs, commencing one third of the way up the appendage and terminating some distance behind tip, also bearing an irregular band of microscopic spinules, beginning in row of hairs and terminating almost at tip. Upper surface—densely hirsute in broader portion. Inner side—basally with very long bipinnate hairs, narrower portion of appendage with row of relatively short bipinnate hairs, also bearing narrow scattered band of microscopic spinules terminating behind tip.

Colour

Alcohol-preserved material: After prolonged preservation most of the smaller specimens without pigment, and largest with orange pigment as follows: Carapace—anterior gastric region, granules on anterior half; chelipeds—upper surfaces generally, inner surfaces of arm and wrist, inner surface of hand on boss at finger articulation and ventral carina, inner surface of immovable finger on proximal quarter of dorsal surface, outer surface of hand on boss at finger articulation. Iridescence present on: carapace—between frontal teeth, between anterolateral teeth, round anterior borders of areas of thin cuticle; chelipeds—general upper surface including movable finger; walking legs—general upper surface of carpus and propodus of all legs; fifth leg—upper surface of distal portion of merus and general upper surfaces of carpus and propodus. An ovigerous ♀ (36 mm, Tosa Bay, S. Japan, 80–120 m, pres. Dr Sakai), bears faint traces of orange pigment as follows: anterior half of carapace closely covered with small spots concentrated densely at edges of unpigmented areas of cervical grooves and of thin cuticle; borders between anterolateral teeth; anterodistal border of arm of cheliped; inner and upper wrist spines; anteroexternal border of wrist (between upper and outer spines); granules on upper surface of hand of larger cheliped; upper outer carina of movable finger. There appear to be no large areas of diffuse pigmentation as shown by the S. African specimen except for a small longitudinal patch behind frontal teeth. The pattern of iridescence differs only in the lack of iridescence from the following: between frontal teeth; round anterior borders of areas of thin cuticle; walking legs and most of fifth leg.

Distribution

Until recently only known from Indonesia and Japan, extended by Grindley (1961) to South Africa and now to Australia. Always from fairly deep water.

Ovalipes molleri (Ward)

Pls 37A, 40B, 41B, 42H; figs 1H, 2G, 3G, 4G

Aeneacancer molleri Ward, 1933, pp. 381–3; pl. XXIII, fig. 11. McNeill, 1953, p. 93; pl. 7, figs 1, 2.

Ovalipes molleri (Ward). Stephenson and Campbell, 1960, pp. 90–1, figs 1D, 2F;9 pl. 2, fig. 3; pl. 5F.

Material examined:—

Australia. New South Wales: ♂ (54 mm), S. of Montague I., coll. K. Moller, Aug., 1929, AM P 10628 (holotype). ♂ (c. 24 mm), ♀ (c. 22 mm), off Tuggerah Lakes, coll. A. A. Racek, 18/vi/1959, 125–145 fm, trawled "Challenge", bottom sand and mud, AM P 14195. 6 ♂♂ (23–31 mm), off Port Stephens, coll. A. A. Racek, 3/viii/1959, 125 fm, mud, otter trawl, AM P 13498. ♂ (33 mm), E. of Port Stephens, coll. A. A. Racek, 3/vii/1959, 110–125 fm, trawled "Challenge", AM P 14185.

Victoria: ♂ (59 mm*), 40 miles SSW. of Mt Cann, 27/viii/1914, 74 fm, AM E 6096 (in company with *O. iridescens*). ♂ (62 mm), c. 30 m W. Babel I., Bass Strait, pres. K. Moller, 80–85 fm, AM P 11415.

Material illustrated: ♂ (59 mm), see * above.

Description

Front: Four toothed (including inner supraorbital lobes); median teeth close together, broadly separate from, and produced further forwards than laterals; median fissure shallow; all teeth sharp; subsidiary lateral lobe on general frontal border, relatively well developed.

Orbit: Upper border not toothed; supraorbital notch fairly deep; suborbital border slightly hairy.

Basal joint of first antenna: Protruding well forwards, with flattened, hirsute, dorsal area.

Basal joint of second antenna: Without flattened dorsal area.

Anterolateral teeth: Five; generally small and sharp, narrow based and broadly separated; between teeth bordered by very fine granules; first tooth largest, blunter than second; second tooth smallest and sharpest.

Carapace: Moderately broad (L/B 1.28); areas generally distinct, with a tubercular elevation on each protogastric region and two, large, reniform areas of very thin cuticle in posterior half; general granulation fine throughout, slightly coarser anteriorly and smooth in the two areas of thin cuticle, in indented areas, and postlateral to them; pterygostomial area with conspicuous, relatively broad striated ridge terminating mesially in rounded granular patch.

Chelipeds: Relatively long, thin, subequal. Arm—anterior border proximally with a few, small, rounded granules, distally with 3–5 sharp spines and 1–3 small sharp tubercles; anterodistal border with large boss; posterior border sparsely and moderately coarsely granular and sparsely hairy; under surface finely granular tending squamiform. Wrist—with short, moderately robust inner spine; upper surface with sharp, well-developed spine at hand articulation and two distinct granular carinae, general upper surface very finely granular; outer surface with two distinct granular carinae, one terminating in a well-developed spine. Hand—slightly swollen; upper surface with distinct boss at wrist articulation, with three granular carinae, outermost very well developed and separating upper and outer surfaces, central one inconspicuous and composed of a sparse line of granules, innermost distally bearing four spines, between outer and central carinae smooth, between central and inner sparsely granular; inner surface with upper border fringed with hairs, with two inconspicuous central, very finely granular carinae and conspicuous lower carina moderately coarsely granular; under surface granular tending squamiform; outer surface dorsally, moderately sparsely and finely granular, central granular carina, ventrally very fine granules in squamiform pattern. Movable finger—upper surface outer margin

bearing densely, moderately coarsely granular, carina, inner margin bearing four sharp well-developed spines increasing in size distally, small spiniform tubercle on inner proximal margin, between margins smooth; inner surface on upper border scattered row of granules and moderately dense fringe of hairs, below this general surface microscopically granular and pitted; outer surface very finely and moderately densely granular. Immovable finger—inner surface with two inconspicuous finely granular carinae, outer surface with two faintly pitted grooves, general surface very finely granular. Both fingers—relatively long and slender with sharp tips and moderately blunt teeth.

Walking legs: First leg: dactyl very long, sharp, with slightly flattened, grooved surfaces and carinate edges; propodus with smooth carina on outer border and smooth ridge near outer surface; carpus with two smooth rounded ridges on outer border. Second leg: dactyl strongly carinate, almost quadriradiate in section; propodus with almost smooth carina on outer border and smooth ridge near outer surface; carpus with smooth rounded ridge on outer border, and barely recognizable rounded ridge near outer surface. Third leg: dactyl strongly carinate, almost quadriradiate in section; propodus with granular carina on outer border; carpus with smooth carina on outer border.

Fifth leg: Carpus with carina on anterior border projecting slightly at distal end; merus moderately broad (L/B 2.07).

Merus of third maxilliped: Surface anteriorly sparsely covered with hairs, posteriorly almost smooth; anterointernal angle slightly produced; anteroexternal angle very obtuse and barely recognizable as an angle; posterointernal surface without distinct raised edge.

Male abdomen: Ultimate segment much broader than long, tip rounded, narrower proximally than in centre and with sharply convex sides, posterior border straight, deeply indented into penultimate segment; penultimate segment slightly longer than broad.

Male first pleopod: Proximal one-third very broad then narrowing abruptly and tapering to tip. Outer side—bearing bipinnate hairs, somewhat scattered and short proximally, then becoming denser and longer distally, terminating well behind tip; also bearing an irregular row of microscopic spinules, beginning in row of hairs and terminating almost at tip. Upper surface—not hirsute. Inner side—bearing bipinnate hairs somewhat scattered in proximal half, slightly denser distally, terminating well behind tip, also bearing narrow scattered band of microscopic spinules terminating behind tip.

Colour

Alcohol-preserved material: After prolonged preservation no pigment visible. Iridescence present on: carapace—between frontal teeth, across anterior portion of carapace, along anterolateral borders, in cervical grooves, around anterior borders of areas of thin cuticle; chelipeds—general upper surface including movable finger; walking legs—small patches on upper surface of merus and propodus of second and third walking legs; fifth leg—general upper surface of merus, carpus and propodus, borders of dactyl, patch also present on ventral surface of propodus.

Distribution

Southeast coast of Australia.

Remarks

Although Sakai (1965, p. 112) states that this species is synonymous with *O. iridescens*, this is not so. The species are immediately separable by the number of frontal teeth.

The O. ocellatus complex

The three forms comprising this complex are very similar and merit re-investigation with more material than is available to us. Previously two forms had been described—*O. ocellatus* and *O. guadulpensis*, but in the present collection some of the specimens previously identified as *O. guadulpensis* possess features of both these species as well as some unique ones. The form of *O. guadulpensis* close to *O. ocellatus* is called *form a* and the other, *form b*.

Features common to all three forms are:

Front: Three toothed (including inner supraorbital lobes); median tooth produced further forwards than laterals; no subsidiary lateral lobe.

Orbit: Upper border not toothed; supraorbital notch deep, suborbital border not or sparsely hairy.

Basal joint of first antenna: Protruding well forwards, with flattened, iridescent, dorsal area.

Basal joint of second antenna: With flattened, iridescent, dorsal area.

Anterolateral teeth: Five; fairly large and robust; narrow based and broadly separated, bordered by moderately coarse granules; first tooth about as sharp as second; fourth the largest.

Carapace: Broad (B/L 1.30–1.31); areas generally not distinct, although with distinct cervical grooves; posterior half either smooth or microscopically granular, smooth in cardiac region; pterygostomial area with conspicuous striated ridge.

Chelipeds: Moderately long, robust, right larger than left. Arm—anterior border proximally striated, distally bearing irregular row of spines; anterodistal border with boss; posterior border densely and finely granular; under surface with rounded granules tending squamiform. Wrist—long with, robust, inner spine and sharp, well-developed outer spine; upper surface without tubercle at wrist articulation; outer surface with finely granular carina leading to spine. Hand—upper surface with boss at wrist articulation, three granular carinae, outermost very well developed and separating upper and outer surfaces, central more feebly developed, inner ending in spine, between carinae predominantly finely granular; inner surface with upper border densely fringed with hairs, bearing granules; under surface granular tending squamiform; outer surface with carina. Movable finger—upper surface with two granular carinae, between carinae granular, and with short granular proximal elevation; inner surface of upper border densely fringed with hairs. Immovable finger—inner surface bearing a row of hairs; outer surface grooved. Both fingers—robust with sharp tips and larger with blunt teeth.

Walking legs: First leg: dactyl long, with slightly flattened, grooved surfaces and carinate edges; propodus with bifurcated carina an outer border; carpus with two smooth ridges on outer border, distally with short ridge near outer surface. Second leg: dactyl with slightly flattened, grooved surfaces and carinate edges; propodus with carina on outer border tending to bifurcate proximally; carpus with smooth carina on outer border. Third leg: dactyl with slightly flattened, grooved surfaces and carinate edges; propodus and carpus with carina on outer border.

Fifth leg: Carpus with carina on anterior border projecting distally; merus broad (L/B 1.82–1.97).

Merus of third maxilliped: Surface generally hairless and bearing conspicuous rounded granules; anterointernal angle strongly produced; anteroexternal angle obtusely rounded; posterointernal surface with distinct raised edge.

Male abdomen: Ultimate segment broader than long, tip rounded, posterior border straight, narrower proximally than in centre and with sharply convex sides, deeply indented into penultimate segment; penultimate segment longer than broad.

Male first pleopod: Proximal two-thirds very broad then narrowing abruptly and tapering to tip. Basal section densely covered with hairs. Outer side—bearing bipinnate hairs becoming very long and dense in the region of narrowing of the pleopod then terminating well behind tip, also bearing band of microscopic granules or spinules beginning where bipinnate hairs finish and terminating well behind tip. Inner side—with dense bipinnate hairs extending from upper surface to edge and terminating some distance behind tip, short scattered irregular row of sharp microscopic spinules terminating just behind tip.

Colour

Hopkins (1963, p. 238) has noted that in both species the fingers of the male are reddish-brown but in the female they are pale yellow to clear white on the outer margins and clear white on the inner. This sexual dichromatism was not apparent in material examined by the authors.

Iridescence: After prolonged alcohol preservation iridescent areas as follows: carapace—the four spaces between anterolateral teeth; cheliped—indentation on posterodistal upper surface of arm, outer wrist spine, proximal elevation on upper surface of movable finger; walking legs—indentation on posterodistal upper surface of merus, anterior edge of carpus and propodus; third maxilliped—ventral surface of carpus, propodus and dactylus; dorsal surface of suborbital tooth; dorsal surfaces of basal joints of first and second antennae.

In dealing below with the three forms, there is little likelihood of confusion between *O. ocellatus* and the remainder, and this species is treated first. The two *O. guadulpensis* forms are not distinguished in the synonymy, and are considered together. Throughout only diagnostic features are listed.

Ovalipes ocellatus (Herbst)

Pls 37B, 40D, 41C, 42I; figs 1I, 2H, 3H, 4H

Cancer ocellatus Herbst, 1799, p. 61, pl. 49, fig. 4.

Portunus pictus Say, 1817, p. 62, pl. 4, fig. 4.

Platyonichus ocellatus (Herbst). Latreille, 1825, p. 152. H. Milne Edwards, 1834, p. 435. de Kay, 1844, p. 9, pl. 1, fig. 1, pl. 5, fig. 7, Smith, 1873, pp. 338 (44), 533 (253). R. Rathbun, 1893, p. 774, pl. 266. Gould, 1841, p. 324.

Platyonychus ocellatus (Herbst). Bell, 1853, p. 84. Milne Edwards, 1861, pp. 415–6; pl. 36, fig. 4. Hector, 1877, pp. 473–4; pl. XXVII, fig. 1. Filhol, 1885, p. 383. Chilton and Bennett, 1929, p. 757.

Ovalipes ocellatus (Herbst). Rathbun, 1898, p. 597; 1905, p. 9. Richardson, 1949, p. 31 (in key). Williams, 1962, pp. 39–40. Bennett, 1964, p. 14.

Ovalipes ocellatus ocellatus (Herbst). Hay and Shore, 1918, pp. 426–7; pl. 32, fig. 7. Rathbun, 1930, pp. 19–23, text fig. 5; pl. 2; pl. 3, figs 1, 2.

Material examined:—

Eastern America: United States: 10 juvs (10–22 mm), Cape Cod Bay, U.S.F.C., 1879, surface, AM P 7437. ♀ (68 mm), off Newport, Rhode I., 1880, USNM. 7 ♂♂ (18–67 mm), 8 ♀♀ (19–40 mm), Fire I., Great South Bay, Long I., 22/IX/1884, USNM. ♂ (85 mm), ♀ (52 mm), Provincetown, Mass., 1899, coll. J. E. Benedict, USNM. 2 ♀♀ (57–60 mm), Vineyard Sound, Mass., April, 1908, AM P 313. ♂

(87 mm*), Edgartown Harbor, Mass., Nov., 1920, AM P 4972. ♀ (42 mm), data as previous specimen, AM P 5030. 5 ♂♂ (25–55 mm), Glynn Co., Georgia, 18/xi/1948, coll. and don. J. Oney, USNM. ♂ (54 mm), "Texas or Florida", coll. L. J. Baughman, USNM.

Locality doubtful. ♂ (48 mm), "Chili", NM.

Material illustrated: ♂ (87 mm), see * above.

Diagnostic features:—

Front: Teeth relatively blunt.

Carapace: Granulation generally even (shared with *O. guadulpensis* form b), but with median longitudinal band of coarse granules extending from mesogastric to anterior cardiac regions (shared with *O. guadulpensis* form a), and with coarse granulations on elevated portions on front half of carapace (shared with *O. guadulpensis* form a).

Chelipeds: Wrist—upper surface finely and densely granular (shared with *O. guadulpensis* form a). Hand—swollen, upper surface between carinae very finely, densely and uniformly granular, inner surface smooth dorsally (shared with *O. guadulpensis* form a) and finely granular ventrally, outer surface smooth or microscopically granular with very finely granular carina. Movable finger—upper surface between carinae very finely and densely granular (shared with *O. guadulpensis* form a), inner surface smooth or microscopically pitted (shared with *O. guadulpensis* form a). Immovable finger—inner surface with relatively sparse row of hairs, and granular (shared with *O. guadulpensis* form b), outer surface smooth or microscopically pitted (shared with *O. guadulpensis* form a).

Merus of third maxilliped: Upper border distinctly curved, anterointernal projection moderately long and broad.

Male pleopod: Inner surface with bipinnate hairs terminating at region of greatest curvature, outer surface with sharp spinules.

Colour

(a) *Alcohol-preserved material.* After prolonged preservation, reddish-brown pigment on: carapace—closely covered by small irregular rings of spots (sometimes faded), smaller in anterior and larger in posterior half, generally fainter in anterior half, also mottled markings bordering frontal teeth and on anterolateral teeth: chelipeds—large scattered spots on upper surfaces of arm and wrist, inner wrist spine diffusely pigmented, upper surface of hand with spots concentrated on two innermost carinae, outermost carinae diffusely pigmented, tubercle at outer finger articulation and distal half of fingers diffusely pigmented.

Iridescence—on borders of frontal teeth (shared with *O. guadulpensis* form b), anterior border of wrist (shared with *O. guadulpensis* form b), general upper surfaces of hand and movable finger (shared with *O. guadulpensis* form b), patches between anterolateral teeth large and diffuse.

(*b*) *Fresh material:* Colour transparency examined by the authors, of fresh ovigerous ♀ from Wood's Hole, Mass., shows pigment on: carapace—closely covered with small irregular rings of dark brown spots, smaller and denser on anterior half. (The following areas without pigment: two patches in each anterior branchial area, cervical grooves.) Chelipeds—upper surfaces of arm, wrist and hand with large scattered black spots, with concentrations on two innermost carinae of hand, inner surface of hand and most of fingers with diffuse orange-red pigment; walking legs—upper surface of merus with scattered spots; fifth leg—merus with scattered spots, propodus and dactyl deep blue bordered by orange or yellow. No obvious iridescence.

Distribution

Rathbun (1930) gives the range from Nova Scotia to South Carolina, and this is repeated by Williams (1962). The present material extends the southern range to Georgia, and doubtfully into the Gulf of Mexico—based on the label "Texas or Florida".

Bennett (1964) includes *O. ocellatus* in his list of species to be excluded from records of New Zealand marine fauna. He states that the recordings of this species by Hector (1877) and by Filhol (1885) repeated by Chilton and Bennett (1929) and by Richardson (1949), were based on incorrect labels, which belonged to specimens actually collected off the eastern coast of the United States of America.

There is no doubt that Filhol's specimen was *O. ocellatus*. Madame D. Guinot has confirmed the identification on our behalf from Filhol's specimen in the Museum National d'Histoire Naturelle, Paris. This specimen is labelled "*Platyonychus ocellatus* Latr. M. Filhol det. Nouvelle-Zealande. H. Filhol 3319–1885 (Mus. d'Otago 1874)". Madame Guinot has kindly provided photographs of the dried specimen which shows the characteristic pigmentation and larger granules in the midline of the carapace The only minor difference compared with material examined is the slightly coarser general granulation of the carapace.

The specimen in the National Museum of Victoria, labelled "Chili", is also almost certainly from an incorrect locality.

Ovalipes guadulpensis (Saussure)

Form a—Pls 37C, 40E, 41D, 42J; figs 1J, 2I, 3I, 4I

Form b—Pls 37D, 40F, 41E, 42K; fig. 1K.

Cancer Ciri Apoa, seu Aratii Pinima, Brasiliensis Seba, 1758, p. 44; pl. 18, fig. 9.

Portunus guadulpensis Saussure, 1858, p. 433 (17); pl. 2, fig. 10.

Platyonichus ocellatus var. Smith, 1886, p. 632.

Ovalipes ocellatus floridanus Hay and Shore, 1918, p. 427; pl. 32, fig. 8.

Ovalipes ocellatus guadulpensis (Saussure). Rathbun, 1930, pp. 23–4, pl. 4. Gunter, 1950, p. 31. Hildebrand, 1954, p. 275.

Ovalipes guadulpensis (Saussure). Williams, 1962, pp. 39–41.

Material examined:—

Form a

Eastern America: 3 juvs (16–20 mm), off Beaufort, N. Carolina, May, 1907, dredged by "Fish Hawk", USNM 51015, ident. by W. P. Hay as "*Ovalipes ocellatus floridanus* sub sp. nov." 4 ♂♂ (56*–65 mm), 3 ♀♀ (56–58 mm), 4 ovig. ♀♀ (57–62 mm), off Jacksonville, Florida, 30° 14′ N., 80° 16′ W., 9/iii/1956, "Bowers", Sta. 32, 40 fm, USNM 99723, ident. F. A. Chace Jr as *O. ocellatus guadulpensis*. ♀ (63‡ mm), SE. off Charleston, S. Carolina, 32° 05′ N., 79° 40′ W., 7/x/1957, "Combat" Sta. 514, Fish and Wildlife, 22–25 fm, USNM 101685, ident. F. A. Chace Jr as *O. ocellatus guadulpensis*.

Material illustrated. ♂ (56 mm), see * above, for line drawings; ♀ (63 mm), see ‡ above, for photographs.

Form b

2 ♂♂ (48, 84 mm), Gulf of Mexico, 30° 21′ N., 87° 00′ W., 13/vii/1957, "Silver Bay", Sta. 24, Fish and Wildlife, 7–8 fm, USNM 101427, ident. F. A. Chace Jr as *O. ocellatus guadulpensis*.

Material illustrated: ♂ (84 mm), for all illustrations except photograph of front (♂ 48 mm).

Diagnostic features:—

Form a

Front: Teeth relatively sharp (shared with form b).

Carapace: Granulation relatively coarse behind frontal and inside anterolateral borders, median longitudinal band of slightly enlarged granules extending from mesogastric to anterior cardiac regions (shared with *O. ocellatus*).

Chelipeds: Wrist—upper surface finely and densely granular (shared with *O. ocellatus*). Hand—not swollen (shared with form b), upper surface between carinae densely granular, mostly fine but occasional large granules, inner surface typically smooth dorsally (shared with *O. ocellatus*) and microscopically granular ventrally, outer surface very finely granular with finely granular carina. Movable finger—upper surface between carinae very finely and densely granular (shared with *O. ocellatus*), general inner surface smooth or microscopically pitted (shared with *O. ocellatus*). Immovable finger—inner surface with relatively dense row of hairs, and partly granular, outer surface smooth or microscopically pitted (shared with *O. ocellatus*).

Merus of third maxilliped: Upper border either straight or very slightly curved, anterointernal projection relatively long and narrow.

Male pleopod: Inner surface with bipinnate hairs terminating just beyond region of greatest curvature, outer surface with sharp spinules.

Colour

Alcohol-preserved material: After prolonged preservation reddish-orange pigment as follows: frontal and anterolateral teeth; but tips of anterolateral teeth white; spines on arm and inside of wrist of cheliped; carinae and larger granules on upper surface of hand; carina on outer surface of hand; dorsal portion of inner surface of hand; variable extents of inner and outer surfaces of both fingers.

Fresh Material—see below

Form b

Front: Teeth relatively sharp (shared with form a).

Carapace: Granulation generally even (shared with *O. ocellatus*), without band of enlarged granules in midline.

Chelipeds: Wrist—upper surface smooth or sparsely granular. Hand—not swollen (shared with form a), upper surface between carinae moderately finely and fairly densely granular, inner surface dorsally with fine scattered granules and moderate to coarse granules ventrally, outer surface granular with inconspicuous granular carina. Movable finger—upper surface between carinae with fine sparse granules, inner surface granular. Immovable finger—inner surface with very dense row of hairs, and granular (shared with *O. ocellatus*), outer surface granular and pitted.

Merus of third maxilliped: Upper border slightly curved, anterointernal projection short and broad.

Male pleopod: Inner surface with bipinnate hairs terminating well beyond region of greatest curvature, outer surface with rounded spinules.

Colour

Alcohol-preserved material: After prolonged preservation orange pigment as follows in large specimen only: general surface anterior half of carapace excluding tips of anterolateral teeth; general anterior surface arm of cheliped including spines;

spine on outer surface of wrist; carinae on upper surface hand; general inner and outer surfaces of hand; general surfaces and especially carinae on movable and immovable fingers.

Fresh material: Williams (1962, pp. 40–1) has described this in detail from North Carolina material, but this cannot be firmly assigned to either of the above forms. His description runs: "General colour of carapace light lavender-grey underlaid with dull yellow, some specimens darker or lighter, with a regular pattern of lighter spots dull yellow, off-white, or bluish yellow to lavender-yellow, rear border of carapace light blue; spines of carapace purplish-red at base to red or purple subdistally, white at tips; carpus and merus of chelipeds somewhat same colour as carpus except pink-flesh coloured at carpo-meral joint and on hand; fingers white on inner surface, and with white teeth; large spine at internal angle of carpus and a few small but distinct spots on superoexternal surface of hand purple, large spine grading to lighter purple on body of carpus; anterior border of chela and first three pairs of walking legs with a longitudinal band of brownish-purple, band extending to lower border of dactyl on chela; dactyls of first three walking legs and outer border of hand immediately below external ridge, same colour, sometimes darker on dactyl with teeth same colour, distal tip of immovable finger similarly coloured; blade of swimming leg yellowish; underparts light. Iridescent spots between anterolateral teeth, on distal or dorsal surface of external carpal spine and along upper edge of hand, at superodistal corner of merus on first three walking legs and along dorsal edge of first three pairs of walking legs distally, on dorsal surface of second abdominal segment; spot between fourth and fifth anterolateral spines nearly semicircular."

The following specimens kindly lent by Dr Austin B. Williams, of the University of North Carolina, were received at a late stage:

Eastern America. 2 ♂♂ (64.5, 82.5 mm), 1 ovig. ♀ (67 mm), 34° 52′ N., 76° 13′ W.—34° 56′ N. 76° 08.5′ W., N. Carolina, 6/xii/1959, roller trawl, m/v "Silver Bay", 7 fm, coll. E. E. Deubler, Jr, UNC Cat. No. 924. 2 ♂♂ (75, 76 mm), 34° 23.5′ N., 76° 24.5′ W.—34° 25′ N., 76° 22′ W., N. Carolina, 6/xii/1959, roller trawl, m/v "Silver Bay" 1.2 fm, coll. E. E. Deubler, Jr, UNC Cat. No. 927. ♀(72 mm), ovig. ♀ (66.5 mm), ESE. Cape Lookout, N. Carolina, 18/i/1963, coll. E. Bayer and N. Coe from fish boats, UNC Cat. No. 1612.

They agree very closely with *O. guadulpensis* form a, apart from the granulation of the inner surface of the hand (as form b). They tend to form b in that most specimens are without the band of enlarged granules in the midline of the carapace, although a few specimens show faint indications of these granules.

VI. INTERRELATIONSHIPS OF SPECIES

a. O. punctatus and Related Species

The close relationship between the following five species—*O. punctatus*, *O. trimaculatus*, *O. catharus*, *O. australiensis*, and *O. elongatus*—are indicated by the fact that the first four had been previously synonymized and the fifth species had been confused with them in collections. *O. georgei*, while separate in many features, shows greater affinity to the above five species than to others in the genus.

These six species are placed in a *group* within the genus (Group A), characterized by possessing the following features, none of which are shown by any of the other species:

1.1 outer supraorbital notch present, and upper border of orbit toothed;
1.2 subsidiary lateral frontal lobe on lower plane than remainder of front;
1.3 anterolateral teeth distinctly large, robust, and broad based;
1.4 pterygostomial area of carapace diffusely granular and without striae;
1.5 chelipeds relatively short;

1.6 anterior border of arm without spines or tubercles;
1.7 posterior border of arm distinctly hairy;
1.8 carina on outer surface of wrist not ending in a spine;
1.9 inner surface of hand with two central carinae, but without lower carina;
1.10 upper surface of movable finger with three carinae;
1.11 upper inner margin of movable finger with row of dense hairs, and below this a carina;
1.12 inner surface of immovable finger with two distinct carinae and two distinct rows of hairs;
1.13 dactyl of first walking leg of male triradiate in section;
1.14 carpus of first walking leg with two carinae on outer border;
1.15 carpus of second walking leg with two carinae (or one carina and one ridge) on outer border;
1.16 carpus of fifth leg without distal projection on carina on anterior border;
1.17 anterointernal projection of merus of third maxilliped short and relatively broad;
1.18 ultimate segment of male abdomen approximately triangular and only slightly broader than long;
1.19 male pleopod evenly curving and tapering throughout, without broad basal area.

Features 1.13, 1.18, and 1.19 are uncertain for *O. elongatus* for which no males are yet available.

The species in this group possess the following additional features in common, but these are shared with other species as indicated:

2.20 four frontal teeth, with medians produced further forward than laterals (shared with *O. molleri*);
2.21 upper surface of hand with pigmented granules (shared with *O. iridescens* and *O. guadulpensis* form a);
2.22 dactyls of second and third walking legs with flattened grooved surfaces and carinate edges but not quadriradiate (shared with *O. ocellatus* subgroup).

b. **Subgroups of Group A**

Within Group A there is a closely related subgroup centred around *O. punctatus*, referred to as the *O. punctatus* subgroup, while *O. georgei* is sufficiently separate from the remainder of Group A to merit a separate subgroup.

(i) *O. punctatus subgroup*

This comprises *O. punctatus*, *O. trimaculatus*, *O. catharus*, *O. australiensis*, and *O. elongatus*, which have the following features in common additional to those of Group A. None of these features are exhibited by other species in the genus.

3.23 subsidiary lateral frontal lobe visible on inner side of lateral lobe;
3.24 basal joint of first antenna without flattened dorsal area;
3.25 under surface of hand with conspicuous striae;
3.26 distal part of merus of first walking leg of male with conspicuous raised collar;
3.27 carpus of fifth leg with sharp, hirsute anterior border;
3.28 pigmented patch in each postlateral area of carapace in preserved specimens which retained colour (in *O. elongatus* more a line than a patch).

Feature 3.26 is uncertain for *O. elongatus*, for which no males are available.

Additional features held in common by the species of the *O. punctatus* subgroup but shared with species outside Group A are:

4.29 carapace areas relatively indistinct (shared with *O. ocellatus* subgroup).

4.30 anterolateral teeth bordered by relatively coarse granules (shared with most of *O. ocellatus* subgroup);

4.31 distinct pigment border just behind edge of frontal teeth (shared with most of *O. ocellatus* subgroup);

4.32 pigmentation present on tubercle of hand of cheliped at wrist articulation (shared with *O. ocellatus* subgroup).

(ii) *O. georgei subgroup*

The distinguishing features of *O. georgei* at the subgroup level comprise negatively the absence of the *O. punctatus* subgroup features, and positively the following:

5.33 subsidiary lateral frontal lobe directly beneath lateral lobe;

5.34 carapace granulation very coarse throughout;

5.35 carapace with mesobranchial area bearing striated ridge;

5.36 anterior half of carapace with four distinct tubercles;

5.37 hand of cheliped coarsely granular on general outer surface;

5.38 carpus of fifth leg with strongly cornified carina on anterior border;

5.39 merus of fifth leg with stout rounded thickening on posterodistal portion of under surface.

Features shared by *O. georgei* and species outside Group A comprise:

6.40 carapace areas very distinct (shared with *O. iridescens* subgroup);

6.41 male abdomen with sides of penultimate segment distinctly convex (shared with *O. iridescens* subgroup);

6.42 pigment on dorsal surface of carapace in large diffuse areas (shared with *O. iridescens* and *O. guadulpensis* form b);

6.43 pigment absent from inner surface of movable finger (shared with *O. molleri*);

6.44 pigment absent from outer surface of movable finger (shared with *O. iridescens* subgroup).

Two features are shared by *O. georgei* and individual species of the *O. punctatus* subgroup. These are:

7.45 upper surface of wrist of cheliped coarsely granular (shared with *O. australiensis*).

7.46 carapace relatively elongate (shared with *O. elongatus*).

c. Remaining Species in the Genus

These comprise two pairs of species, viz. *O. iridescens* and *O. molleri*; and *O. ocellatus* and *O. guadulpensis* with its two forms, a, and b. These species possess a sufficient number of features in common to merit the status of a major grouping (Group B) with the following features in common:

8.47 upper border of orbit not toothed, and outer supraorbital notch absent;

8.48 pterygostomial area of carapace striated;

8.49 arm of cheliped with spines or tubercles on anterior border;

8.50 outer surface of wrist with carina ending in a spine;

8.51 hand of cheliped with carina at lower border on inner surface;
8.52 dactyl of first walking leg of male not triradiate in section, but long, sharp, with flattened grooved surfaces and carinate edges;
8.53 carpus of first walking leg with two smooth ridges on outer border;
8.54 carpus of second walking leg with one carina (or ridge) on outer border;
8.55 carpus of fifth leg with distal projection on carina on anterior border;
8.56 iridescence on carapace and chelae.

(i) *O. iridescens subgroup*

Each of the two pairs of species in Group B is sufficiently distinctive to merit subgroup status. The first subgroup, comprising *O. iridescens* and *O. molleri*, is referred to as the *O. iridescens* subgroup.

The species possess the following features held in common, additional to those of Group B. None are exhibited by other species of the genus.

9.57 subsidiary lateral frontal lobe on general frontal border and almost forming a submedian lobe;
9.58 dorsal area of basal joint of first antenna flat;
9.59 anterolateral teeth slender, not robust;
9.60 anterolateral teeth bordered by fine sparse granules;
9.61 carapace with areas of very thin cuticle;
9.62 chelipeds relatively very elongate;
9.63 arm of cheliped with posterior border sparsely granular;
9.64 wrist with three spines;
9.65 wrist with short inner spine;
9.66 wrist with fine granules on general upper surface;
9.67 hand with four large spines on upper inner margin;
9.68 movable finger with four or more large spines on upper inner surface;
9.69 movable finger with carina present on upper outer surface;
9.70 fingers slender;
9.71 dactyls of second and third walking legs strongly carinate and almost quadriradiate in section;
9.72 merus of third maxilliped without distinct raised edge on posterointernal surface;
9.73 merus of third maxilliped with short narrow anterointernal projections;
9.74 male pleopod with basal one half to one third broad, then narrowing abruptly with sharp curvature on outer side.

Additional features shared by species in the *O. iridescens* subgroup, but also shared with species outside Group B, are:

10.75 carapace areas very distinct (shared with *O. georgei*); feature 6.41 relisted.
10.76 general inner surface of hand smooth, not microscopically granular (shared with *O. punctatus*);
10.77 male abdomen with sides of penultimate segment distinctly convex (shared with *O. georgei*); feature 6.41 relisted.
10.78 pigment absent from outer surface of movable finger (shared with *O. georgei*); feature 6.44 relisted.
10.79 relatively elongate carapace (shared with *O. elongatus* and *O. georgei*).

(ii) *O. ocellatus subgroup*

The species in this subgroup (*O. ocellatus* and *O. guadulpensis* forms a and b) possess the following features in common, additional to those of Group B. None are exhibited by other species of the genus.

11.80 no subsidiary lateral frontal lobes;
11.81 lower border of orbit either without hairs or sparsely hairy;
11.82 basal joint of second antenna with iridescent dorsal area;
11.83 anterolateral teeth robust but relatively narrowly based;
11.84 anterolateral teeth bordered by moderately dense coarse granules;
11.85 first anterolateral tooth about as sharp as second;
11.86 chelipeds moderately long;
11.87 arm of cheliped with striated anterior proximal border;
11.88 hand of cheliped without distinct middle carina on outer surface;
11.89 movable finger with two distinct carinae on upper surface;
11.90 movable finger with outer surface either bearing miscroscopically granular carina or without carina;
11.91 propodus of first walking with bifurcate carina on outer border;
11.92 propodus of second walking leg with carina on outer border tending to bifurcate;
11.93 merus of third maxilliped with granular surface and at most sparsely hirsute;
11.94 merus of third maxilliped with very conspicuous long and broad antero-internal projection;
11.95 male pleopod with basal two-thirds broad then narrowing abruptly with sharp curvature on outer side.

Features held in common with the *O. ocellatus* subgroup, but shared with species outside Group B, are:

12.96 carapace areas relatively indistinct (shared with *O. punctatus* subgroup), feature 4.29 relisted;
12.97 anterolateral teeth bordered by relatively coarse granules (shared with *O. punctatus* subgroup), feature 4.30 relisted;
12.98 pigmentation present on tubercle of hand of cheliped at wrist articulation (shared with *O. punctatus* subgroup); feature 4.32 relisted.
12.99 dactyls of second and third walking legs with flattened grooved surfaces and carinate edges but not quadriradiate (shared with Group A); feature 2.22 relisted.

Features shared by the *O. ocellatus* subgroup and individual species of the *O iridescens* subgroup are:

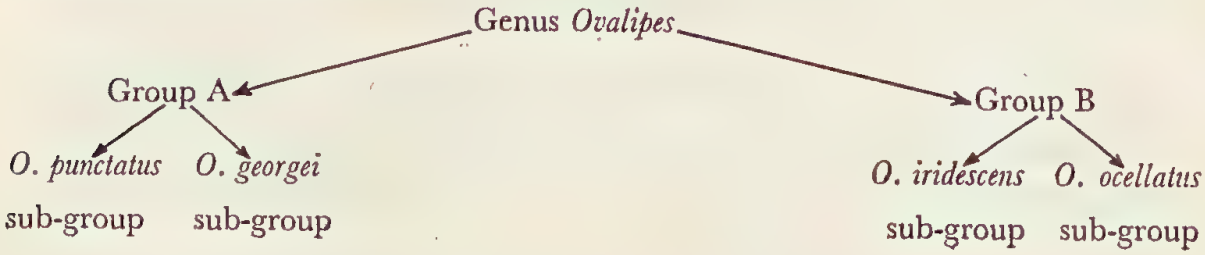
13.100 three frontal teeth (shared with *O. iridescens*);
13.101 arm of cheliped with posterior border finely granular and without hairs (shared with *O. iridescens*);
13.102 arm of cheliped with faint squamiform markings on under surface (shared with *O. molleri*);
13.103 immovable finger without carinae on outer surface (shared with *O. molleri*);
13.104 iridescence on dorsal area of basal joint of first antenna (shared with *O. molleri*);
13.105 discrete iridescent areas between anterolateral teeth (shared with *O. iridescens*).

Discussion of Interrelationships

If the genus is to be split into formal taxonomic enities, Groups A and B should be given an appropriate formal status. The former possesses nineteen unique features and the latter ten of the basis of the present study. Against this Group A shares three additional features with species from Group B, and there are six further features shared between subgroups or individual species. Because of these "cross-links", it seems preferable at this stage to keep the genus intact even at the subgeneric level.

It should be noted that the subgroups of Group B each have a large number of diagnostic features, sixteen in the case of the *O. iridescens* subgroup and the same number in the *O. ocellatus* subgroup. If a "splitting" technique was applied to its limit each of these subgroups, and, therfore, presumably all the subgroups, could be given generic status. If so, the generic name *Ovalipes* would be restricted to the *O. ocellatus* subgroup because *O. ocellatus* is the type species of the genus (Rathbun, 1898). The *O. iridescens* subgroup would then become the genus *Aeneacancer* Ward (1933), while new generic names would have to be given to both the *O. punctatus* subgroup and to *O. georgei.*

The interrelations between the groups and subgroups can be expressed diagrammatically as follows:



VII. DISCUSSION

Ovalipes is primarily an antitropically distributed genus, with four sub-groups, three of which show parallels between systematic affinities and biogeography. The remaining sub-group, containing only *O. georgei*, is known from two specimens from Western Australia.

In the *O. punctatus* sub-group there was considerable confusion in the synonymy. The majority of workers had synonymized all the species with *O. bipustulatus* (H. Milne Edwards, 1834), and later with *O. punctatus* (de Haan, 1833) following Rathbun (1930). However, Milne Edwards' material is actually *O. trimaculatus* (de Haan, 1833). Examination of all available material necessitated the division of this sub-group into five species, viz., *O. punctatus*, *O. trimaculatus*, *O. australiensis*, *O. catharus*, and *O. elongatus.*

With the exception of *O. trimaculatus*, each has a localized distribution as follows: *O. punctatus* from Japan and China, *O. australiensis* from Australia, *O. elongatus* from Lord Howe Island and Kermadec Islands, and *O. catharus* from New Zealand and southern Australia. *O. trimaculatus* has a wide cool-water Southern Hemisphere distribution comprising eastern and western South America, eastern and western South Africa, and the Indian Ocean.

The *O. iridescens* sub-group includes the only tropical recordings in the genus. *O. iridescens*, while known from widely separated areas, has been recorded from deep water in the Banda Sea where surface water temperatures are relatively low, c. 27° C (Rochford, 1962). In contrast, *O. molleri* is as yet known only from a restricted Australian area.

The *O. ocellatus* sub-group contains relatively shallow water Atlantic species which merit further investigation. Williams (1962) re-elevated *O. guadulpensis* to its original specific status, but of the characters he used for separation the following seem to vary: evenness of carapace granulation, size and shape of anterolateral iridescent spots, and granulation of the carina on the outer surface of the hand of the cheliped. Within the limited series of *O. guadulpensis* material here examined, there appear to be two forms. Many of the features used for the separation of these two forms show similarities with *O. ocellatus*. It is possibly significant that one of the forms is from the Gulf of Mexico and the other from the Atlantic. Extensive series of *O. guadulpensis* should be examined, particularly Brazilian material, which presumably is geographically separate from the remainder.

Although stridulating structures are known in other genera of portunids, for example *Portunus vocans* (A. Milne Edwards, 1878) and *P. nipponensis* (Sakai, 1938), it is in *Ovalipes* that they reach their best development—all species possessing stridulating mechanisms. In "*O. punctatus*" Guinot-Dumortier and Dumortier (1960) stress sound production by the striated undersurface of the hand of the cheliped engaging with the modified merus of the first pair of walking legs. They discount Balss' (1921) suggestion that the modified dactyl of the first leg is also engaged with the striae, but examination of preserved material throughout all the species of the *O. punctatus* sub-group convinces us of the reality of Balss' concept. Yet further stridulating possibilities are conceivable in these species, and it is hoped to detail them in a later paper. Meanwhile, for the sake of simplicity the *O. punctatus* sub-group may be described as stridulating species which use the ridges under the hand of the cheliped.

Meanwhile, in the *O. ocellatus* sub-group, the main stridulating structures are the striated pterygostomial regions of the carapace, engaged by the arm of the cheliped (Hansen, 1921; Balss, 1921; Guinot-Dumortier and Dumortier, 1960). In the *O. iridescens* sub-group, as Miers first noted, there are pterygostomial striae as in the *O. ocellatus* sub-group, but in this case they are engaged, not by the arm of the cheliped, but by the ischium. In *O. georgei* there is a quite different stridulating structure, apparently unique amongst Crustacea, of ridges on the posterior half of the carapace which are engaged by the fifth leg.

If the presence of stridulating structures is taken as a feature of the genus, it is difficult to understand why there should be three different types of striated structures, with one type (pterygostomial striae) engaged by two different kinds of plectra. It is possible that the genus is a polyphyletic group, but against this is the great similarity in general form and the coherence of the distributional picture. The only alternative seems to be to assume that the ancestral *Ovalipes* had a predisposition towards stridulation.

It is hoped to discuss this possibility in a later paper.

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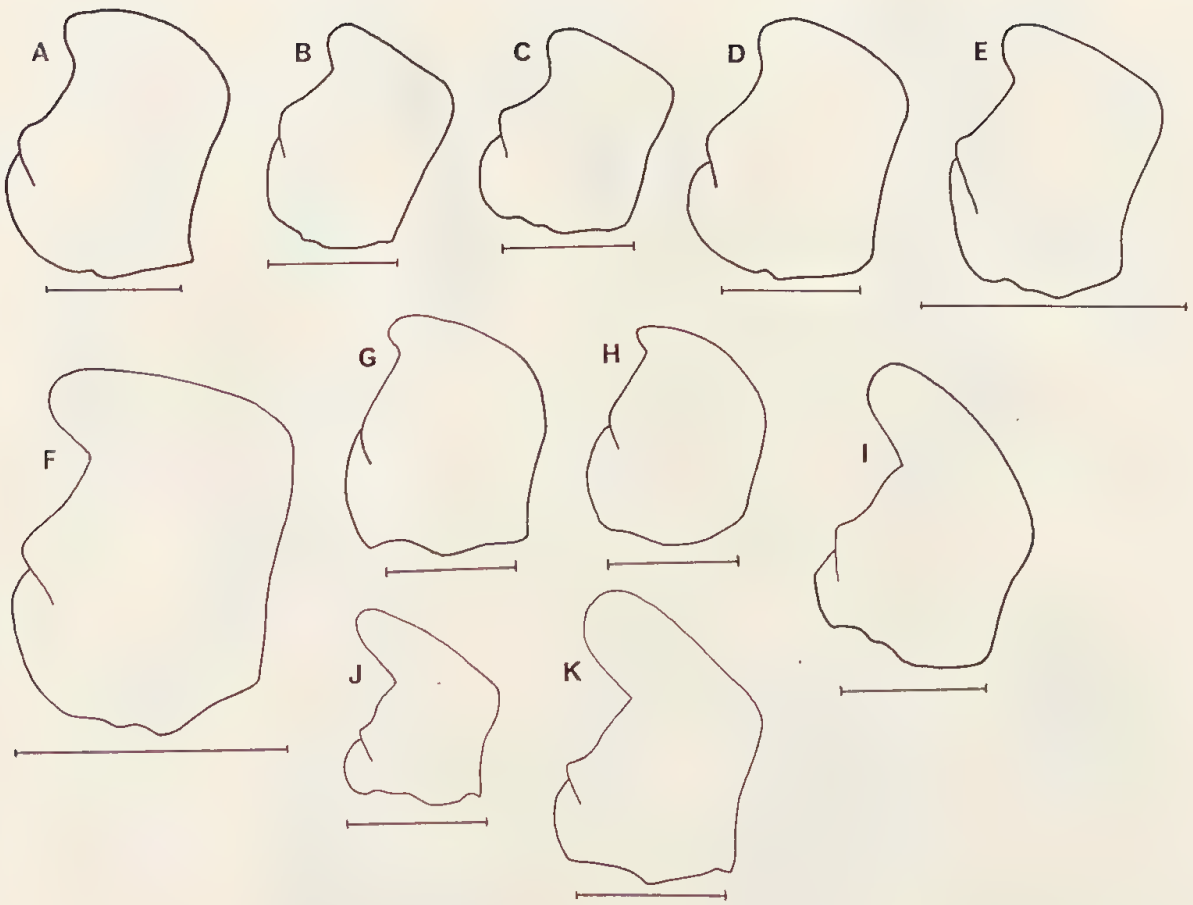


Fig. 1.—Meri of left third maxillipeds, anteroventral views, distal portions on top of drawings, bristles not shown. Scale, 5 mm. A. *Ovalipes punctatus;* B. *O. trimaculatus;* C. *O. catharus;* D. *O. australiensis;* E. *O. elongatus;* F. *O. georgei;* G. *O. iridescens;* H. *O. molleri;* I. *O. ocellatus;* J. *O. guadulpensis* form a; K. *O. guadulpensis* form b.

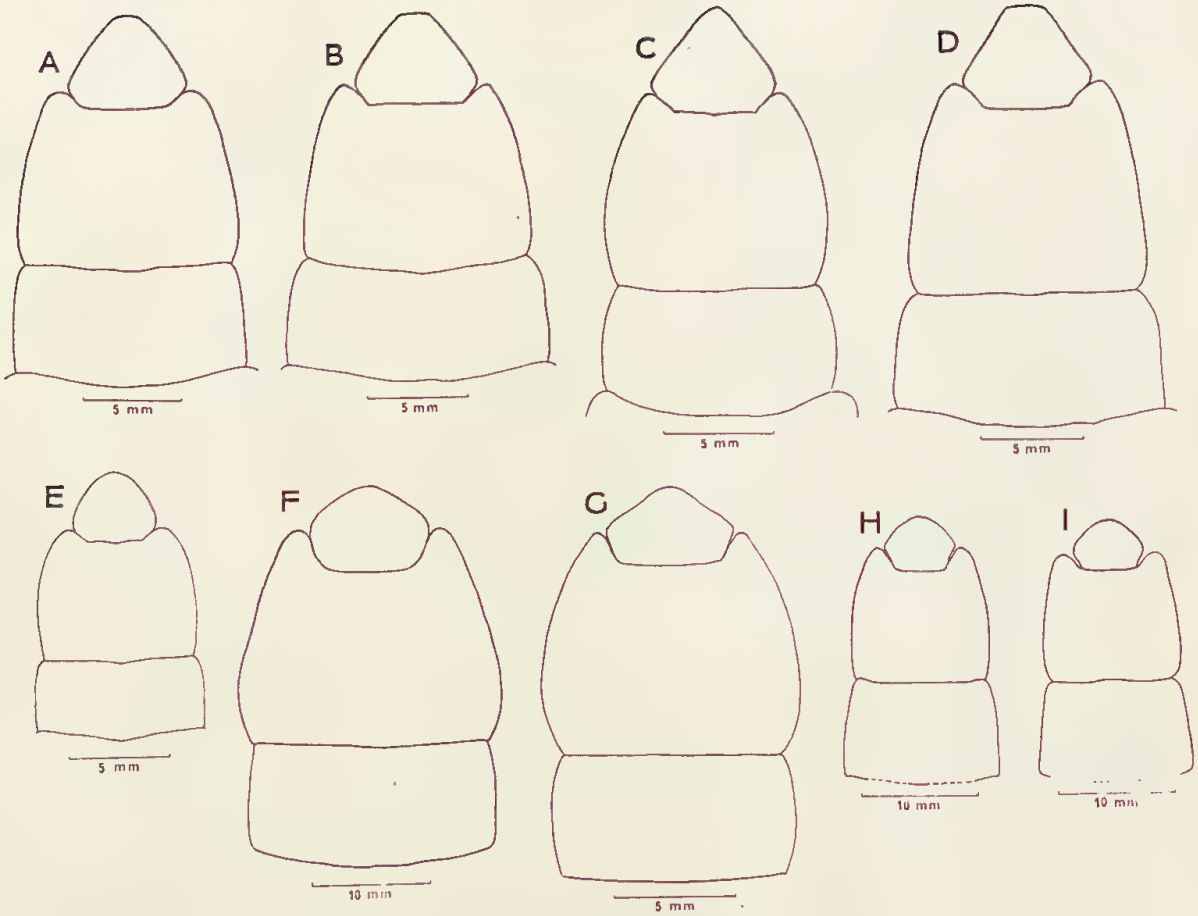


Fig. 2.—Male abdomens. A. *Ovalipes punctatus;* B. *O. trimaculatus;* C. *O. catharus;* D. *O. australiensis;* E. *O. georgei;* F. *O. iridescens;* G. *O. molleri;* H. *O. ocellatus;* I. *O. guadulpensis* form a

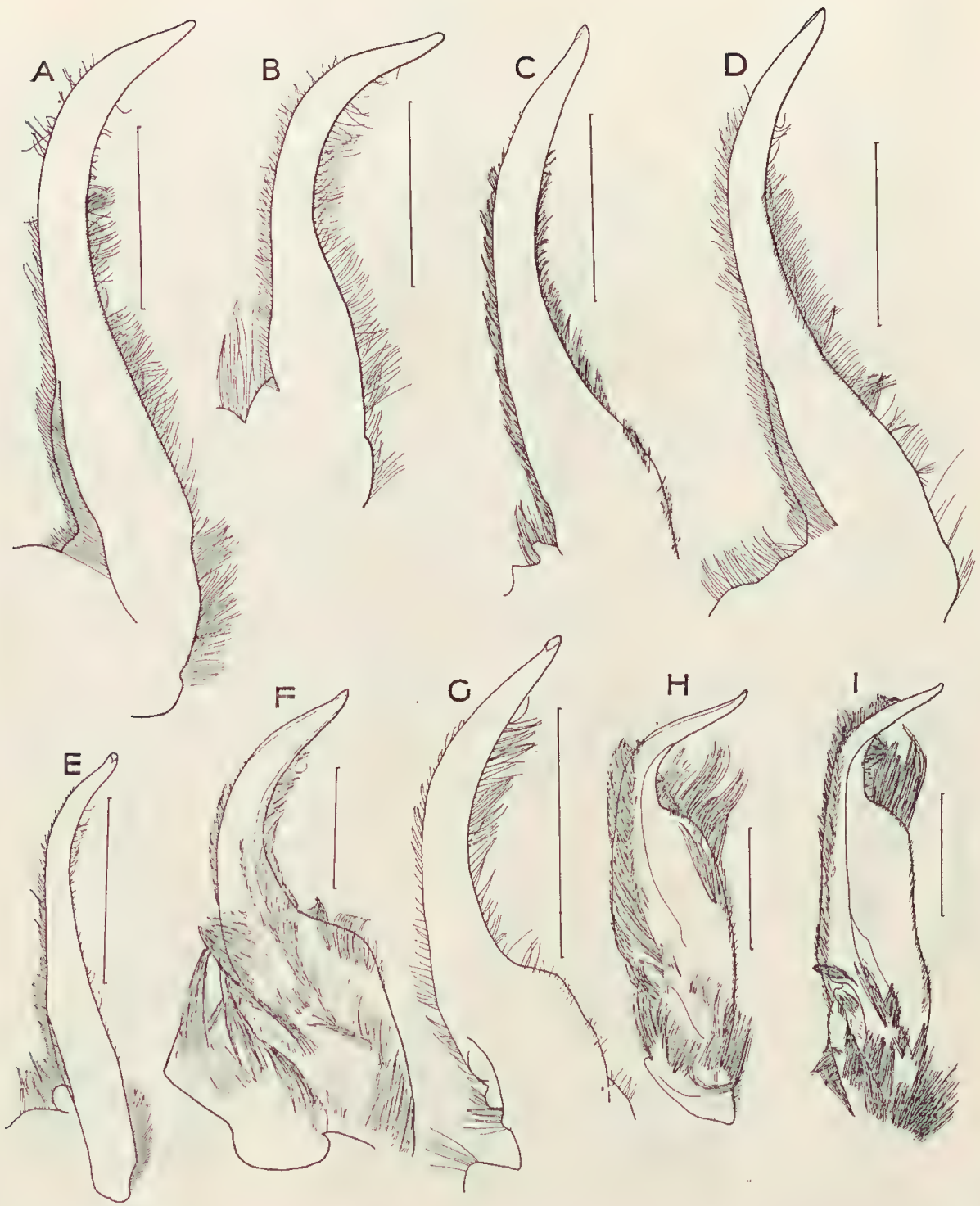


Fig. 3.—Low power views of upper surface of first male pleopod from left side. Scale, 5 mm. A. *Ovalipes punctatus;* B. *O. trimaculatus;* C. *O. catharus;* D. *O. australiensis;* E. *O. georgei;* F. *O. iridescens;* G. *O. molleri;* H. *O. ocellatus;* I. *O. guadulpensis* form a.

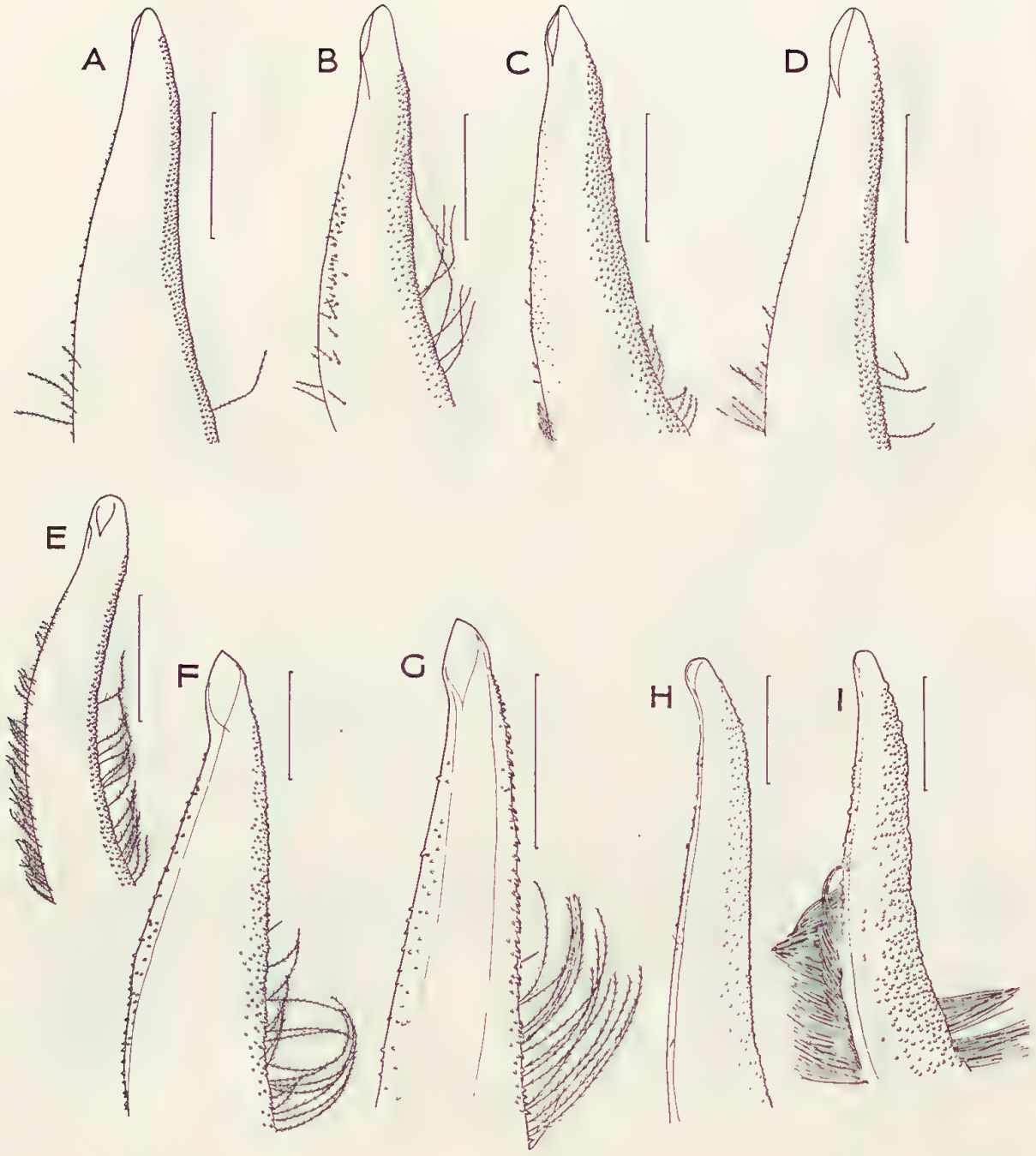


Fig. 4.—High power views of upper surface of first male pleopod from left side. Scale, 1 mm. A. *Ovalipes punctatus;* B. *O. trimaculatus;* C. *O. catharus;* D. *O. australiensis;* E. *O. georgei;* F. *O. iridescens;* G. *O. molleri;* H. *O. ocellatus;* I. *O. guadulpensis* form a.

EXPLANATION OF PLATES

Plate 35. Dorsal views; scale for A–C, 1 div. – 1 mm; D, distance between white dots – 5 mm. A. *Ovalipes punctatus* (de Haan); B. *O. trimaculatus* (de Haan); C. *O. australienses* n. sp.; D. *O. australiensis* n. sp., juvenile.

Plate 36. Dorsal views; scale, 1 div.=1 mm. A. *Ovalipes catharus* (White); B. *O. elongatus* n. sp.; C. *O. georgei* n. sp.; D. *O. iridescens* (Miers).

Plate 37. Dorsal views; scale, 1 div.=1 mm. A. *Ovalipes molleri* (Ward); B. *O. ocellatus* (Herbst); C. *O. guadulpensis* (Saussure) form a; D. *O. guadulpensis* (Saussure), form b.

Plate 38. Hand of cheliped. A. *Ovalipes punctatus* (de Haan) outer surface; B. *O. punctatus* (de Haan), under surface; C. *O. trimaculatus* (de Haan), outer surface; D. *O. trimaculatus* (de Haan), under surface; E. *O. catharus* (White), outer surface; F. *O. catharus* (White), under surface.

Plate 39. Hand of cheliped. A. *Ovalipes australiensis* n. sp., outer surface; B. *O. australiensis* n. sp., under surface; C. *O. elongatus* n. sp., outer surface; D. *O. elongatus* n. sp., under surface; E. *O. georgei* n. sp., outer surface; F. *O. georgii* n sp., under surface.

Plate 40. A. *Ovalipes iridescens* (Miers), outer surface of hand of cheliped; B. *O. molleri* (Ward) outer surface of hand of cheliped; C. *O. georgei* n. sp., fifth leg; D. *O. ocellatus* (Herbst), upper surface of hand of cheliped; E. *O. guadulpensis* (Saussure) form a, upper surface of hand of cheliped; F. *O. guadulpensis* (Saussure) form b, upper surface of hand of cheliped.

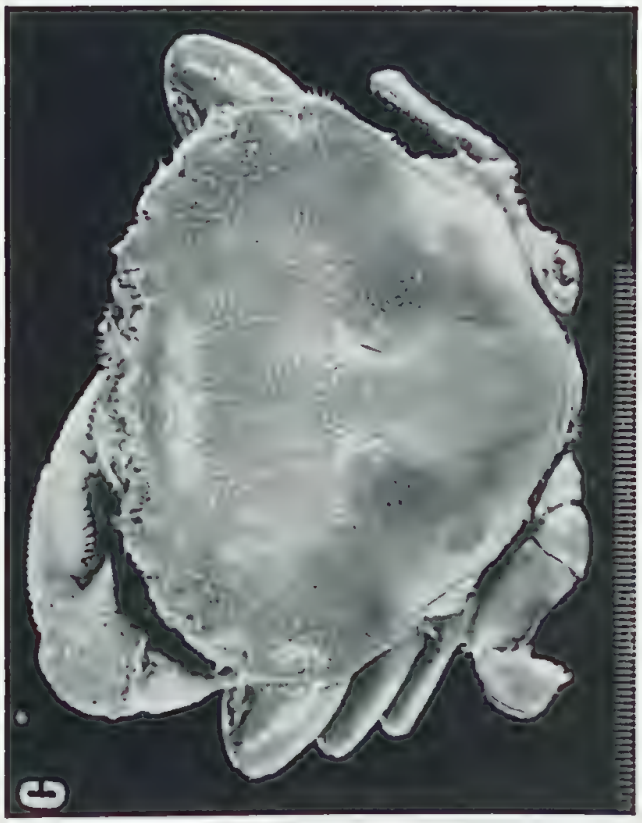
Plate 41. A–E. Ventral surface of carapace showing pterygostomial ridge (pr), and ischium and proximal part of merus of cheliped; A. *Ovalipes iridescens* (Miers); B. *O. molleri* (Ward); C. *O. ocellatus* (Herbst); D. *O. guadulpensis* (Saussure) form a; E. *O. guadulpensis* (Saussure) form b. F. *O. australiensis* n. sp., dactyl of first walking leg of male, showing tricarinate tip; G. *O. australiensis* n. sp., distal part of merus and proximal part of carpus of first walking leg of male showing meral collar. Merus on left, carpus on right.

Plate 42. Front of carapace showing frontal teeth, orbits, and first anterolateral teeth. A. *Ovalipes punctatus* (de Haan); B. *O. trimaculatus* (de Haan); C. *O. catharus* (White); D. *O. australiensis* n. sp.; E. *O. elongatus* n. sp.; F. *O. georgei* n. sp.; G. *O. iridescens* (Miers); H. *O. molleri* (Ward); I. *O. ocellatus* (Herbst); J. *O. guadulpensis* (Saussure) form a; K. *O. guadulpensis* (Saussure) form b.

B

D

A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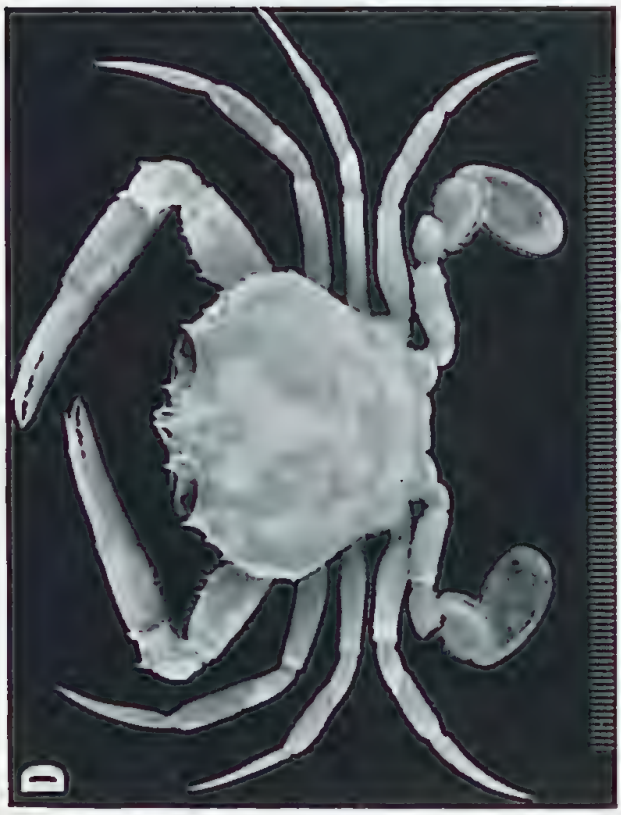
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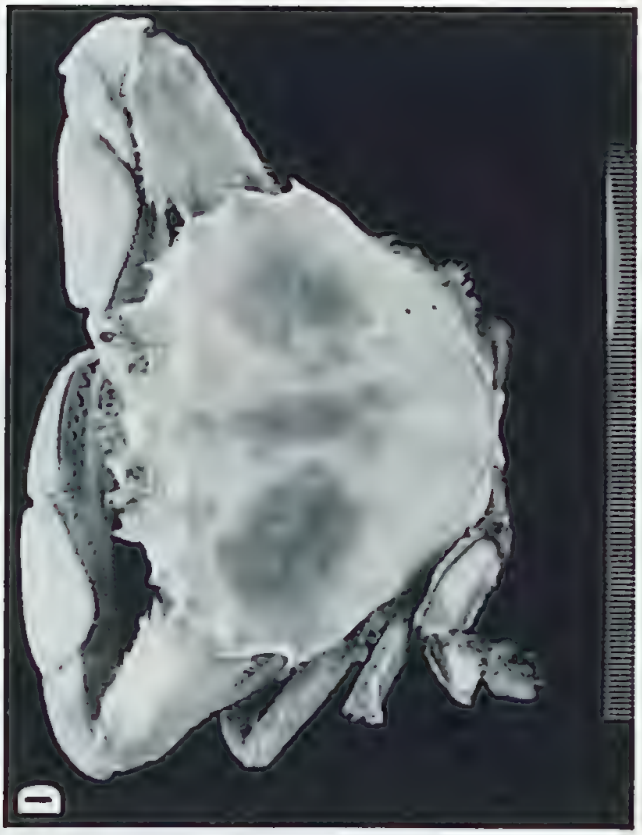
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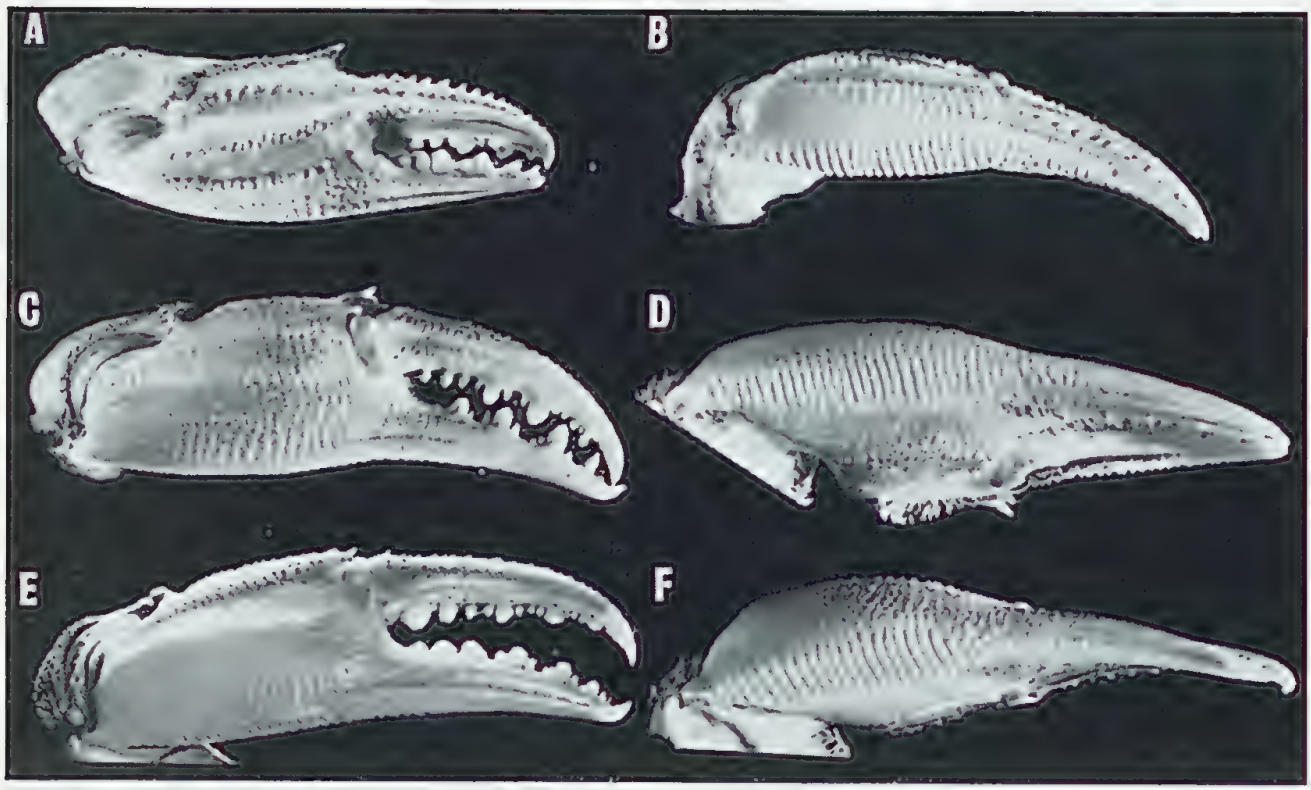
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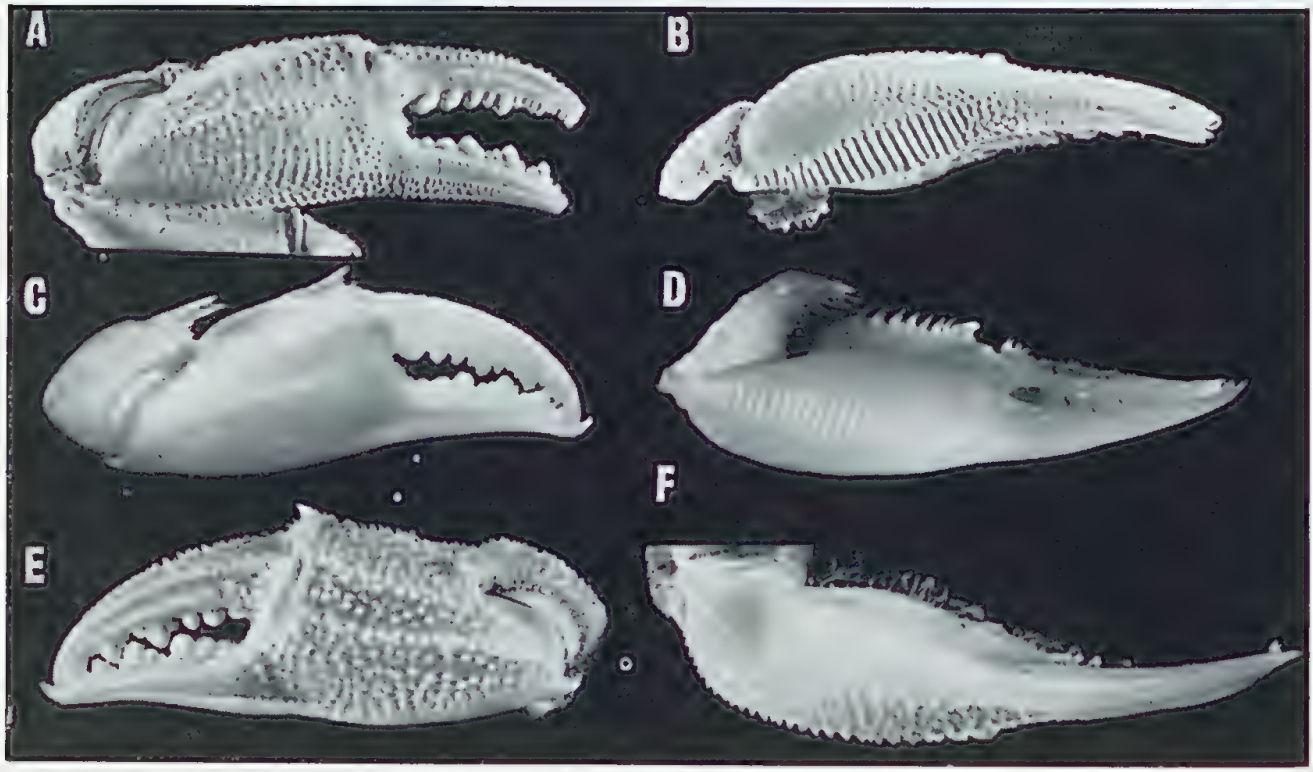
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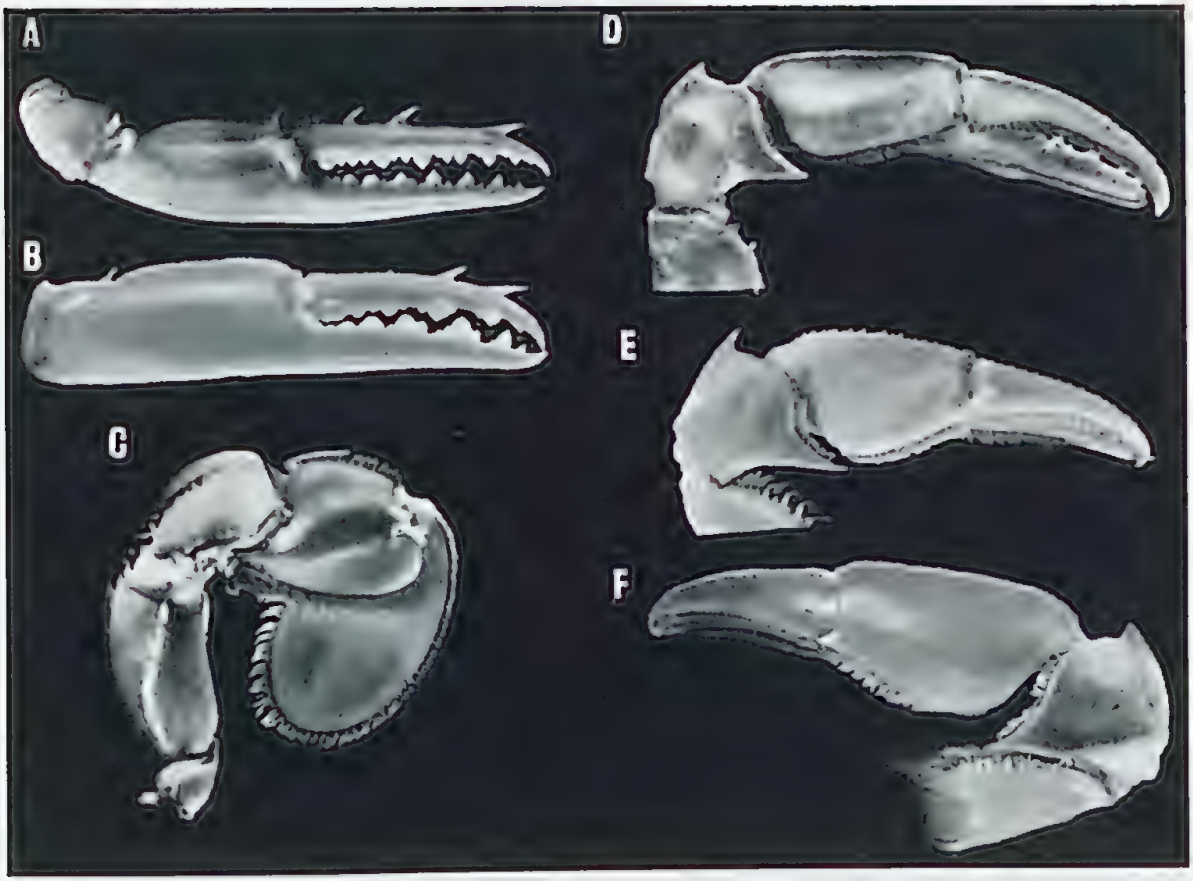
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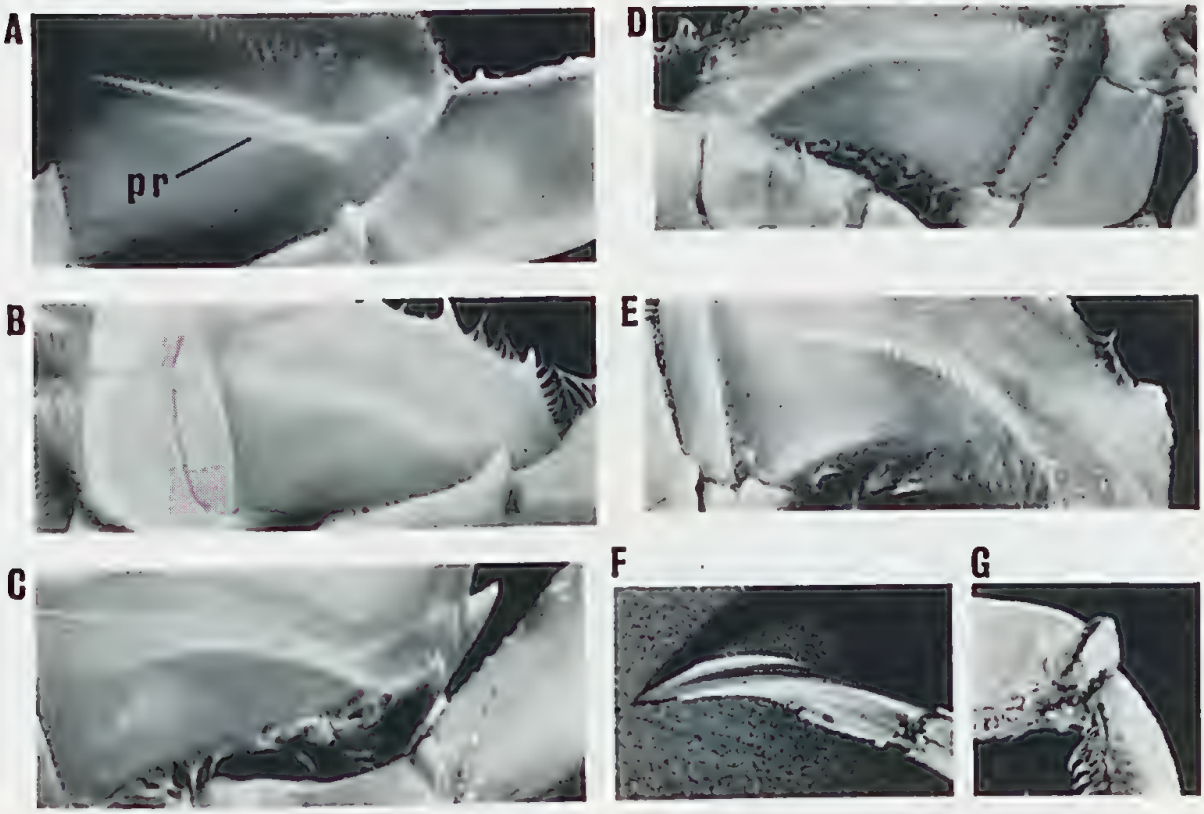
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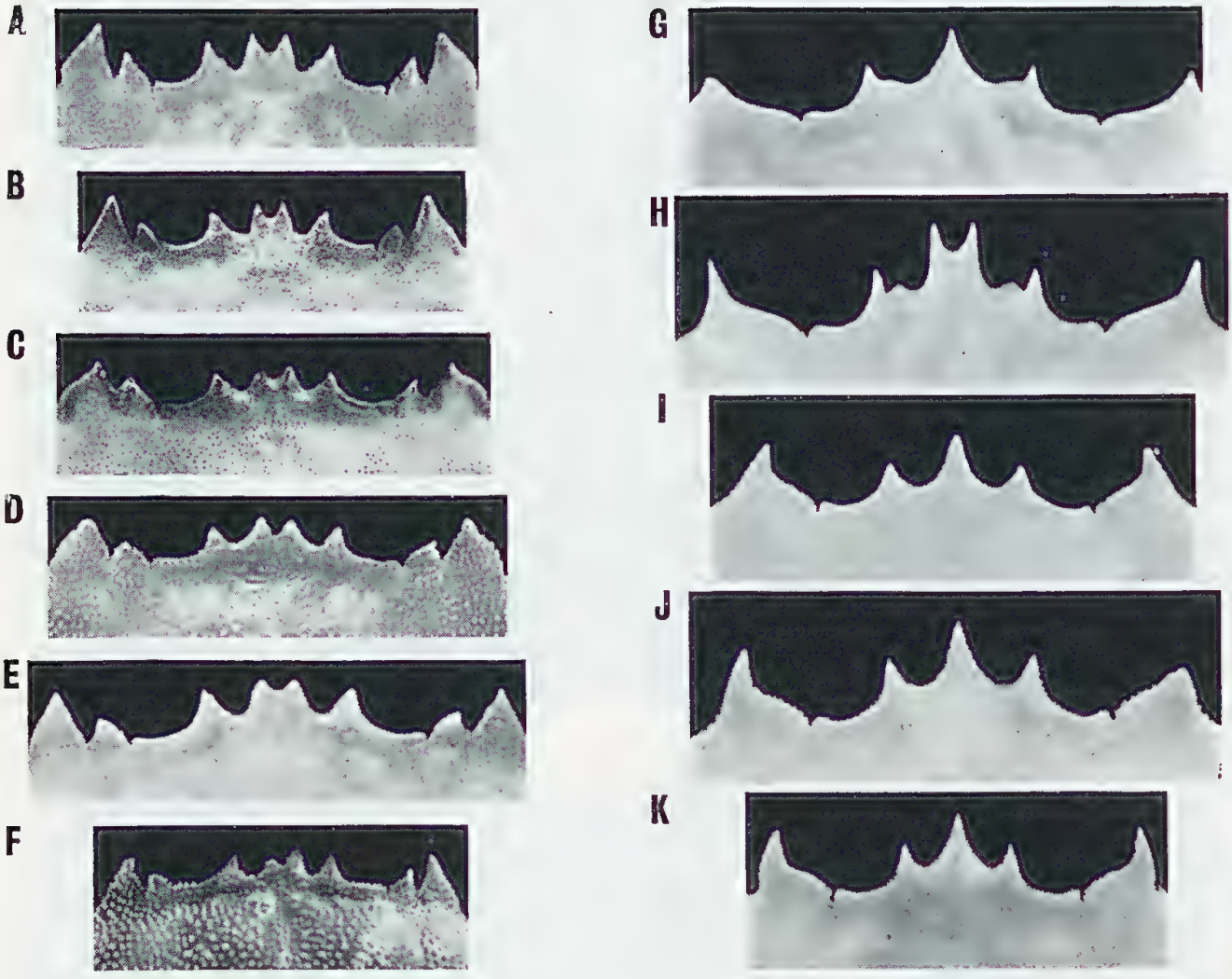
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THE GENUS *CAIRNSIMYIA* MALLOCH (Diptera, Heleomyzidae, Rhinotorini)

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Figures 1-26

Manuscript received, 13th September, 1967

Synopsis

The known species of the genus *Cairnsimyia*, all of which occur in Australia and New Guinea (including Papua and West Irian), are described and a key is given for their identification. Six of the nine species are described as new. The larva of one species is also described. The family Rhinotoridae is reduced to a tribe of the family Heleomyzidae.

Introduction

The subfamily Rhinotorinae was proposed by Williston (1896) within the family Ropalomeridae (often incorrectly spelled Rhopalomeridae) and was elevated to family rank by Hendel (1916). Most authors, however, continued to regard it as a subfamily of the Ropalomeridae until recently, when Brues, Melander, and Carpenter (1954), Wheeler (1954), and Steyskal (1957) have advocated family status for the Rhinotoridae. Hennig (1948) placed this group in the Lauxaniidae but later (1958) regarded it as a distinct family related to the Heleomyzidae, pointing out the numerous differences separating it from the Ropalomeridae.

The author (McAlpine, 1958) referred the Australian genus *Cairnsimyia* Malloch, originally described as a heleomyzid, to the Rhinotoridae, and almost simultaneously Hennig (1958) commented on its similarity to that family.

Faunal treatises and texts including keys to families of Diptera almost invariably exclude the Rhinotoridae as a distinct family, though its members cannot be run to Ropalomeridae in keys. Brues, Melander, and Carpenter (1954) include Rhinotoridae at two points in their key to the families of Diptera. None of the species will run to the first point in their key, though most of the neotropical ones may be run to the second. The separation of the Trixoscelidae from them is very imperfect, as in many of these the subcosta is less developed than in the Rhinotoridae.

This group is here reduced to a tribe, the Rhinotorini, within the family Heleomyzidae, for reasons which are explained below.

Some notable characters of the Rhinotorini, which illustrate its close relationship to other Heleomyzidae, are as follows: vibrissae are present, though the elongation of the face may make the position of the vibrissal angle obscure; convergent postvertical bristles occur in *Rhinotoroides* and in some species of *Cairnsimyia;* preapical tibial bristles are often present, though short, in *Cairnsimyia;* the costa is broken near the termination of the subcosta.

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Location of Specimens

The following abbreviations are used below to indicate the collections in which material is located:

AM	Australian Museum, Sydney.
BM	British Museum (Natural History), London.
CSIRO	Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Canberra.
DEI	Deutsches Entomologisches Institut, Eberswalde, East Germany.
NMV	National Museum of Victoria, Melbourne.
QM	Queensland Museum, Brisbane.
SAM	South Australian Museum, Adelaide.
SPHTM	School of Public Health and Tropical Medicine, University of Sydney.
UQ	Entomology Department collection, University of Queensland, Saint Lucia, Brisbane.
USNM	United States National Museum, Washington, D.C.

Acknowledgements

Miss Kathleen English, who has added much to the knowledge of Australian dipterous larvae, is responsible for discovering the larvae of *Cairnsimyia* here described. Mr J. C. Deeming, formerly of the British Museum (Natural History), provided information on the types of Walker's two species, thus preventing the publication of unnecessary synonyms. Dr G. Morge and Dr C. W. Sabrosky provided information on specimens in the Deutsches Entomologisches Institut and United States National Museum respectively, and Mr B. H. Cogan and Mr K. G. V. Smith supplied information regarding labels on specimens in the British Museum (Natural History).

Family **HELEOMYZIDAE** Loew

Tribe **Rhinotorini** Williston new status

Vertex of head excavated, cheeks very broad; postverticals often small or absent; orbits usually rather short, with one or two reclinate fronto-orbital bristles; antennae porrect, with compact, rounded third segment; distal section of proboscis elongate, with reduced labella. Dorsocentrals 1 or 2; propleural small or absent; mesopleuron bare or haired, sometimes with weak posterior bristles. Preapical tibial bristles very short or absent. Costa without major spines, sometimes variably weakened beyond hm; Sc approximated to vein 1, sometimes obsolete at extreme apex; submarginal cell (R_3) usually narrower than first posterior cell (R_5) at apex; vein 6 not reaching margin. Male abdomen with tergite 6 greatly reduced.

The above characters distinguish the tribe from other groups within the Heleomyzidae. The relationship to the genera *Anastomyza* Malloch and *Apophoneura* Malloch is so close that the author has considered including these in the Rhinotorini. They are, however, distinguished by the following characters: vertex not excavated; costa with prominent spaced spines on anterior surface. In the Rhinotorini, as in most other heleomyzids, there is a series of close set thick black spinules on anterior surface of costa, but only in *Cairnsimyia cavifrons*, among the species of this tribe seen by the author, is there an additional anterior series, consisting of a few small spinules at irregular intervals beyond end of subcosta.

The author maintains that the tribe Rhinotorini is an extreme development of that branch of the Heleomyzidae which includes *Anastomyza* and *Apophoneura*. A study of the species of the genus *Apophoneura* reveals that most of the peculiar characters of the genus *Rhinotora* are foreshadowed, often in a less exaggerated form, in all or

some of these species. The author presents a list of these *Rhinotora*-like characters which he has observed in the genus *Apophoneura* (many of which also occur in species of *Anastomyza*).

1. Slight tendency of vertex of head to become depressed and eyes to bulge posteriorly (most noticeable in *A. exquisita* Malloch).

2. Cheeks widened in comparison with most other Heleomyzidae.

3. A strong bristle near middle of cheek, usually in addition to a posterior cheek bristle corresponding to that of *Diplogeomyza*, *Suillia*, etc.

4. Distal section of proboscis somewhat elongate, with shortened labella.

5. Arista tending to be inserted at or beyond middle of third antennal segment (e.g., *A. superba* Malloch).

6. Dorsocentral bristles reduced to two pairs.

7. Scutellum somewhat elongate (in *A. exquisita* Malloch and *A. superba* Malloch).

8. Short spinescent bristles present on ventral surface of fore femur (in males of *A. exquisita* Malloch and *A. punctipennis* Malloch).

9. Preapical tibial bristles much reduced or indistinct (especially so in *A. recurrens* Malloch).

10. Spaced anterior costal spines may be scarcely longer than anterodorsal series of coastal spinules (in *A. picta* Malloch).

11. Crossveins present between costa and vein 2 (in *A. exquisita* Malloch, *picta* Malloch, *punctipennis* Malloch, and *superba* Malloch).

12. Cerci of males fused.

Wheeler (1954) has defined the Rhinotoridae as having the subcosta complete, from his examination of specimens of *Rhinotora diversa* Giglio-Tos. His figure, however, shows the subcosta not quite reaching the costa. In the four neotropical species available to the author —*Rhinotora pluricellata* Schiner, *R. diversa* Giglio-Tos, *Rhinotoroides bifurcata* Lopes, and *Neorhinotora mutica* (Schiner)—the subcosta is obsolete or indistinctly pigmented for a short distance before reaching the costa.

The tribe occurs in the warmer parts of the Neotropical Region (genera *Rhinotora*, *Rhinotoroides*, and *Neorhinotora*) and in New Guinea and eastern Australia as far west as South Australia and including Tasmania (genus *Cairnsimyia*). The neotropical genera are more closely related to one another than to *Cairnsimyia* and together they undoubtedly form a separate monophyletic unit. Evidence of this is provided in the following table:

Characters of Neotropical and Australasian Genera

Neotropical	Australasian
An outstanding isolated postgenal bristle	No postgenal bristle, but a series of marginal cheek bristles present
2 dorsocentral bristles	1 dorsocentral bristle
Presutural bristle strongly developed	Presutural bristle absent or minute
Scutellum bare or minutely pubescent	Scutellum setulose
Subcosta apically indistinct	Subcosta distinct throughout
Cerci of ♂ fused and joined laterally to edges of epandrium	Cerci of ♂ free or fused but not joined laterally to epandrium

Morphology of the Protandrium

The protandrium consists of those segments of the abdomen of a male fly which lie between the preabdomen (usually segments 1–5 in the Schizophora) and the genital segment or hypopygium (segment 9). Irregularities of the sclerites of this region occur in the higher Diptera (Cyclorrhapha) as a result of the rotation of the genital segment through a complete circle. This may result in a simple spiral displacement of tergites and sternites of the protandrium as seen in some Coelopidae. More often there is reduction or fusion of the sclerites, which, in extreme cases, tends to restore external symmetry.

The study of the rhinotorine protandrium raises several interesting problems if approached from the orthodox method of seeking to homologize its visible parts. In attempting to identify these parts the author has made the three following observations:

1. Some structures are clearly secondary sclerotizations of the cuticle and not homologous with tergites or sternites.

2. Whilst individual spiracles are presumably homologous with those from the sixth and seventh pairs of less specialized Diptera, there is in some cases no clear existing evidence of their identity.

3. The existing sclerites, even when distinguished by discontinuity or visible lines of fusion, are often not readily interpreted as exact homologues of tergites or sternites. It is probable that these parts became partly fused or otherwise modified so far back in evolutionary history as to have lost their exact identity. The nomenclature here used for the sclerites should be taken as giving only an approximate indication of their probable homologies.

The protandria of three genera have been investigated in the present study: *Neorhinotora* [represented by *N. mutica* (Schiner), fig. 9]; *Rhinotora* (represented by *R. pluricellata* Schiner, fig. 10); *Cairnsimyia* (several species examined, see fig. 11). Steyskal (1957) has described and figured the protandrium of *Rhinotora diversa* Giglio-Tos.

In illustrating the protandria I have used a method devised by Steyskal (1957 and elsewhere). They are shown as if split along the median ventral line and then spread flat. The broken lines at the sides of the diagrams represent the median ventral line, and that in the centre the median dorsal line.

In all genera tergite 6 is reduced and more or less fused with the dorsally placed sternite 8. Sternites 6 and 7 are displaced to the left side and connected to sternite 8, which is always well developed. Apart from these general similarities, the conformation of the sclerites is very diverse.

In *Neorhinotora* tergite 6 is well defined and joined antero-dorsally to sternite 8. The sixth left spiracle is contained within its left lateral limits. A partly detached piece on its right lateral extremity contains the sixth and seventh right spiracles, each of which may be identified from the fact that one lies posteriorly to the other. A narrow secondary sclerotized band runs completely round the ventral surface and is joined to the anterolateral margin of tergite 6 on each side. Sternites 6 and 7 are less clearly joined to the dorsal complex than in other forms of the tribe. Sternite 7 is joined to sternite 8 by a narrow band upon which the seventh left spiracle is situated. In the degree of independence of tergite 6 this might be considered to be the least specialized of the forms here described. On the other hand, it possesses the symmetrically formed secondary ventral band of segment 6, an extraordinarily specialized structure only known in neotropical species of Rhinotorini.

The protandrium of *Rhinotora pluricellata* is similar in some respects to that of *Neorhinotora* but is more specialized and more nearly approaches a symmetrical condition. Tergite 6 has become largely desclerotized in the mid-dorsal region and what remains of it is fused with sternite 8. However, the secondary ventral band is well developed, extending downwards from each side and continuing around the ventral surface. Sternites 6 and 7 are weakly developed on the left side and merge with sternite 8 at their dorsal extremities. The large sternite 8 contains the spiracles of the sixth and seventh pairs, and, as these are situated one above the other, it is not possible to identify the spiracles individually.

In *Cairnsimyia* the structure suggests evolution along somewhat different lines. The existing sclerites are fused into a single highly asymmetrical mass, the greater part of which is situated on the dorsal surface. In *C. robusta* this includes tergite 6, whilst in *C. uniseta* tergite 6 is free. Tergite 6 is displaced further to the right than usual, and in *C. robusta* is seen to include 2 spiracles on the right side and 1 on the left. Sternite 6 occupies a lateroventral position and sternite 7 is laterally placed, serving to connect sternite 6 to the dorsal sternite 8. Along the anterior margin of sternites 6 and 7 there is a heavily sclerotized strip, which may have some relationship to the ventral band of the neotropical forms, but differs in being asymmetrical, confined to the left side, and fused to the sternites for its full length.

Genus **Cairnsimyia** Malloch

Cairnsimyia Malloch, 1931: 294.

Head strongly excavated on vertex, the ocellar and postocellar regions slightly convex within the excavation; cheeks broad; face concave in profile, protuberant on middle of lower margin, extended laterally below cheeks; prelabrum prominent; fronto-orbital bristles one or two, rather short; postverticals often small or absent, convergent when present; vibrissae and usually some long cheek bristles present; proboscis slender with small labella. Antenna porrect, with short, inconspicuous first segment; second segment short, truncate, third segment rounded, tumid; arista long, with variable minute pubescence.

Thorax broad; mesoscutum extensively setulose; disc of scutellum setulose; presutural bristle minute or absent; one dorsocentral; four strong scutellars; propleural weak or replaced by fine hairs; mesopleuron haired, sometimes one or more of the posterior hairs developed into a bristle; two to four sternopleurals and some fine hairs on upper part of sternopleuron; prosternum with one or more pairs of hairs or setulae. Legs rather short and stout; preapical dorsal tibial bristles very small or absent. Wings extensively patterned with brown spots, without supernumerary crossveins; costa broken only at end of subcosta, with spaced spines short and weak or absent, a series of closely placed black spinules on its dorsal surface; subcosta strongly developed but very close to vein 1 throughout, sometimes fused with vein 1 at extreme tip; vein 2 long; vein 4 strongly angled at junction with anterior crossvein; second basal and anal cells complete; anal crossvein curved; vein 6 not nearly reaching wing margin.

Abdomen short and broad. Male postabdomen with tergite 6 narrow, displaced towards right side, more or less fused with sternite 8 or quite free; sternite 6 ventral, largely contained in an invagination of the cuticle above sternite 5, joined to the lateral sternite 7 which in turn is joined to the dorsal sternite 8; one pair of articulated surstyli; cerci separate or fused.

Type species: *Cairnsimyia cavifrons* Malloch.

Key to Species of **Cairnsimyia**

1. Ocellar and humeral bristles minute or absent; prelabrum with median process or prominence; Papua ..... *aroana* nov.

   Ocellar and humeral bristles long and strong; prelabrum without process or distinct prominence 2

2. Two fronto-orbitals; all femora with thickened spine-like ventral bristles; propleuron without erect hairs near centre; in male, anterior paramere (pregonite) large with 1 or 2 terminal spines 3

   One fronto-orbital; femora without thickened bristles or spines; propleuron with fine erect hairs near centre; in male, anterior paramere undeveloped 5

3. Two or three brown spots in costal cell; surstylus of male somewhat narrowed basally, the produced anterior distal angle not recurved; female postabdominal segments normal, telescopic, without spine-like marginal bristles on sternite 5; Queensland, New South Wales, Victoria, Tasmania and South Australia ..... *robusta* (Walker)

   No spots in costal cell; surstylus and female postabdomen variable 4

4. Wing with numerous distinct brown spots; surstylus very attenuated basally, the produced anterior distal angle recurved; female abdomen with all segments behind the fourth forming the lining of a gaping cup-shaped cavity; Queensland ..... *excavata* nov.

   Wing with very indistinct pale-grey spots; surstylus not much attenuated basally, broadened and elbowed before middle, with slender distal part projecting forwards, female postabdomen normal, folding telescopically; New South Wales ..... *sydneiensis* nov.

5. Prescutellar acrostichals absent; third antennal segment horizontally ovoid; arista variable 6

   Prescutellar acrostichals present; third antennal segment not longer than high, almost circular; arista not thickened, brown 7

6. Arista somewhat thickened, with dense white pubescence; West New Guinea ..... *inscripta* (Walker)

   Arista slender with very inconspicuous pubescence; New Guinea *crosskeyi* nov.

7. Mesopleuron with one or more long setulae on extreme posterior margin; ocellar spot not extending in front of ocellar triangle; veins conspicuously paler in region of basal cells; Queensland, New South Wales ..... *cavifrons* Malloch

   Mesopleuron without prominent setulae on posterior margin; a large blackish patch surrounding ocelli; wing veins only paler at extreme base 8

8. Postverticals well developed, about as long as the fronto-orbitals; surstyli obliquely oval, about twice as long as wide; Queensland, New South Wales ..... *verticalis* nov.

   Postverticals very small; surstyli spatulate, about three times as long as maximum width; Queensland, New South Wales, Victoria *uniseta* nov.

Cairnsimyia robusta (Walker) new comb.

(Figs 1, 11, 14, 22–26)

Heteromyza robusta Walker, 1853: 403.

This species is closely related to *C. excavata* (described below) but differs in the black sternopleural bristles, spots in the costal cell and structure of male and female postabdomens.

♂ postabdomen with surstylus stout, curved, slightly narrowed bassally, truncate distally with anterior angle prominent and posterior angle rounded off; hypandrium with a rounded lateral lobe, at the base of which is a series of horizontal grooves; a short, setulose process just in front of lateral lobe; anterior paramere prominent, elongate, with three short, thick setulae on inner surface at base and two terminal, claw-like, finely acuminate spines; posterior paramere small, concealed from the side by lateral section of hypandrium, with about 5 fine terminal spines; aedeagus with terminal section shorter than in *C. excavata;* cerci completely fused into a small, conical, haired process.

♀ postabdomen of the normal telescopic form; no spines on sternite 5; cerci slender.

Dimensions: total length, ♂ 3.6–5.6 mm, ♀ 3.9–4.7 mm; length of thorax, ♂ 1.8–2.3 mm, ♀ 1.9–2.4 mm; length of wing, ♂ 3.5–4.8 mm, ♀ 3.5–5.0 mm. Reared specimens are not included in these measurements as most are abnormally small.

Last instar larva (fig. 22) elongate-fusiform, tapered posteriorly, the terminal segment produced into a short siphon; surface of cuticle smooth. Anterior spiracle (fig. 25) with numerous short branches arising from the elongate central axis; posterior spiracles (fig. 26) on separate short tubercles at end of siphon, each spiracle with 3 broad oval openings containing short lamellae just within the aperture, surrounded by 4 groups of flattened hydrophobe hairs, some of which are branched. Anterior margins of abdominal segments 2–7 with well developed creeping pads armed with numerous short, stout, slightly hooked spines; abdominal segment 1 and the 3 thoracic segments with a few rows of spines on anterior margins of their ventral surfaces, there being only 3 rows of spines on prothorax (fig. 24); anal region without a spinose pad. Head region (fig. 24) completely surrounded by a fringe of slender, soft appendages which are long, tentacle-like, and particularly numerous at sides; anterior part of head region with the usual 2 pairs of papillae, the upper one being that considered by many dipterists to represent the antennae; an additional 2 pairs of sensory papillae at each side of atrial opening, and a pair of simple process at posterior margin of this area; a pair of tooth-like processes between these simple papillae; a pair of plates on each side of atrial opening, which bear serrated transverse ridges; a pair of unpigmented but heavily ridged, sclerotized plates on posterior margin of atrial opening near base of mouth-hooks, which may represent the dentate sclerites. Cephalopharyngeal skeleton as shown in fig. 23, with pigment distributed as in that figure; mouth hooks simple; a pair of small rod-like sclerites between and below anterior arms of hypostomal sclerite; a small dorsal plate above hypostomal sclerite; floor of pharyngeal sclerite with longitudinal folds.

Distribution: southeastern Queensland; eastern New South Wales; Victoria; coastal South Australia; Tasmania.

Material examined (adults)—Queensland: Brisbane, October, 1928 (3 ♂, 3 ♀, UQ), F. A. Perkins; Caloundra, August, 1929 (1 ♀, UQ), F. A. Perkins. New South Wales and Australian Capital Territory: Kurrajong, October, 1958 (1 ♂,

AM), D. K. McAlpine; Hornsby, near Sydney, October, 1957 (1 ♂, 3 ♀, SPHTM), D. J. Lee; Roseville, near Sydney, reared, February, July, August, 1958–1962 (11 ♂, 12 ♀, AM, 2 ♂, 2 ♀, USNM), K. English; Vaucluse, near Sydney, January, 1963 (1 ♂, AM), C. V. Nathan; Gundamaian, Royal National Park, January, 1926 (1 ♂, CSIRO), I. M. Mackerras; Waterfall, Royal National Park, April, 1925 (1 ♀, CSIRO), I. M. Mackerras; Black Mountain, Canberra, February, 1960 (1 ♀, CSIRO), I. F. B. Common. Victoria: Warburton, January, 1924 (3 ♂, SPHTM), F. E. Wilson; Mordialloc, January, 1918 (♂, ♀ in copula, NMV), no collector's name. South Australia: Sleaford Bay, near Port Lincoln, March, 1961 (1 ♀, CSIRO), J. Casanova. Tasmania: Launceston, January, 1914 (1 ♀, SAM); Mangalore, near Hobart, January, 1913 (1 ♂, 1 ♀, BM), A. White.

Holotype: Van Dieman's Land (BM), re-examined by J. Deeming.

Habitat: dry sclerophyll forest, partly cleared country, and suburban gardens. The larvae were found by Miss K. English in tunnels made by cerambycid larvae in a fig tree in her garden. Pupation took place within the tunnel near the entrance.

Cairnsimyia sydneiensis sp. nov.

(Figs 2, 13, 16)

♂ ♀: head yellowish-buff; frons, except the orbits and triangle, brown; a brown patch extending both in front of and behind ocelli; brown spots at bases of fronto-orbital and vertical bristles; all cheek hairs pale. Antenna yellow-brown, darker above. Prelabrum and palpi light yellow-brown. Thorax, light reddish-brown; mesoscutum with 4 somewhat ill-defined longitudinal greyish-buff bands of the same colour behind suture, these bands tending to merge in parts, and a narrow median such band posteriorly; pleura with a longitudinal pale-buff band from centre of propleuron to upper part of pteropleuron, and less distinct bands from lower part of propleuron to metathoracic spiracle and on upper part of sternopleuron; hairs on mesopleuron pale except for a few brown ones near posterior margin; hairs on sternopleuron all pale. Legs light yellowish, the femora, especially the hind ones, variably suffused with yellowish-brown; tibiae with a brown band before middle and one near distal end which may be narrow and subterminal or broader and reaching apex of tibia. Wing (fig. 2) with spots that are pale greyish, rather indistinct, and fewer than in *C. excavata*, *robusta*, and *uniseta;* no spots in costal cell. Abdomen yellowish-brown.

General structure very similar to that of *C. excavata* (see below). Fronto-orbital bristles shorter and weaker than in that species, the anterior one sometimes duplicated.

Sternopleural bristles usually 1 or 2, unpigmented. Femora with well developed anteroventral and posteroventral series of spines, except for the anteroventral series on fore femur which is much reduced; a short preapical dorsal bristle sometimes distinguishable on fore tibia. Wing with submarginal cell not much narrower than marginal cell for most of its length.

♂: postabdomen with surstylus strongly bent forward before middle, tumid posteriorly at the bend, distal part directed forward, more slender than basal part; anterior paramere large and prominent, directed outwards and forwards, with some long setulae anteriorly and shorter ones towards base posteriorly, and with a large horizontally flattened articulated terminal claw; posterior parameres very small and scarcely visible without dissection; aedeagus as in fig. 16B; cerci fused, setulose.

♀: postabdomen folding telescopically; segment 5 large and exserted; sternite 5 with some short black spines near posterior margin; cerci slender, haired.

Dimensions: total length, ♂ 5.4 mm, ♀ 5.4–5.8 mm; length of thorax ♂ 2.5–2.6 mm, ♀ 2.6–3.0 mm; length of wing, ♂ 5.4–5.5 mm, ♀ 5.7–6.2 mm.

Distribution: New South Wales—central coast district.

Material examined: Sydney, 18th October, 1938 (holotype ♂, paratypes, 3 ♀, CSIRO, 1 ♂, 1 ♀, AM), A. D. Gill; Gundamaian, Royal National Park, January, 1926 (paratype ♀, CSIRO), A. J. Nicholson.

Cairnsimyia excavata sp. nov.

(Figs 3, 15)

♂ ♀: head brownish-grey; cheeks yellowish; frons, except the orbits and frontal triangle, brown; a brown blotch enclosing the ocelli and extending well behind them; fronto-orbital bristles and sometimes also the inner vertical bristle arising from brown spots; all cheek hairs pale. Antennae yellow-brown, darker above; prelabrum brown; palpi yellowish. Mesoscutum and scutellum grey with rusty-brown markings, a darker brown mark on each side above humeral callus and another just above wing base; scutellum pale yellowish at apex; pleura reddish-brown, with thin greyish dusting on most of surface, a conspicuous creamy-white band extending from middle of propleuron to about middle of pteropleuron, and a blotch of similar colour on lower part of propleuron; mesopleuron with fine pale hairs, sometimes a few darker ones on posterior margin. Legs yellow-brown; tibiae each with a sub-basal and subapical darker brown band. Wing (fig. 3) with numerous greyish-brown, mostly rounded spots, absent in costal cell. Abdomen rusty-brown, the tergites more yellowish towards their distal margins and greyish towards lateral margins.

Head with vertex more broadly and shallowly excavated than in *C. cavifrons* and *C. uniseta;* two fronto-orbitals, the anterior one slightly shorter; ocellars long, proclinate about twice as widely separated from each other as are the two posterior ocelli; postverticals absent; usually only one short brown or black cheek bristle behind vibrissa; third antennal segment as high as long; arista appearing bare with normal magnification, but with sparse minute hairs visible at a magnification of x200.

Humeral bristle well developed; prescutellar acrostichal absent; scutellum flattened, broadly rounded, the bristles evenly spaced; propleuron without long hairs near centre but with very short, dense pubescence in this region; propleural bristle reduced to a weak pale hair; sternopleural bristles usually 3, often unpigmented in male. Fore femur with series of strong posteroventral spines and weaker anteroventral spines; middle and hind femora with strong anteroventral spines and usually some weaker posteroventral spines; preapical tibial bristles not distinguishable. Wings rather narrow; submarginal cell much narrower than marginal cell for most of its length.

♂: postabdomen with surstylus much narrowed basally, expanded and curved forwards distally making the anterior margin deeply concave; anterior paramere large, and very prominent, elongate, with a long, obtuse terminal black spine, and two or three hairs anteriorly, one of which is long and curved; posterior paramere small with a few fine terminal spines; aedeagus slender basally with the usual swollen sclerotized terminal section; cerci joined ventrally, with numerous rather long hairs.

♀: postabdomen greatly modified, not telescopic; all segments behind segment 4 forming the lining of a large cavity, with what appears to be tergite 5 divided into a pair of oval sclerites; cerci not apparent.

Dimensions: total length, ♂ 4.0–4.4 mm, ♀ 4.6–5.0 mm; length of thorax, ♂ 1.9–2.1 mm, ♀ 2.2–2.3 mm; length of wing, ♂ 4.1–4.5 mm, ♀ 4.8–5.0 mm.

Distribution: southern Queensland—tablelands.

Material examined: Stanthorpe, 26th August, 1925 (holotype ♂, QM, paratypes, 1 ♂, 1 ♀, AM, 2 ♂, 2 ♀, UQ), F. A. Perkins.

Cairnsimyia verticalis sp. nov.

(Figs 4, 17)

♂ ♀ : agreeing with the description of *C. uniseta* in all characters except the length of the postverticals and the structure of the male terminalia.

Postverticals well developed, about as long as fronto-orbital bristles, convergent or crossed.

♂ with abdominal tergite 6 reduced and scarcely visible on the left side; both spiracles of sixth and seventh pairs present. Surstylus almost oval, less than twice as long as maximum width, anterior margin more convex than posterior margin, the apex with numerous, dense, short spines, mainly on inner surface, elsewhere with fairly long setulae. Parameres short, bispinose apically; no additional processes on hypandrium. Cerci small, short-haired, fused.

♀ with normal terminal segments and slender cerci.

Dimensions: total length, ♂ 3.9–4.3 mm, ♀ 4.5–4.8 mm; length of thorax, ♂ 1.8–2.2 mm, ♀ 2.3–2.4 mm; length of wing, ♂ 3.6–4.7 mm, ♀ 4.6–5.0 mm.

Distribution: southern Queensland; northern New South Wales.

Material examined—Queensland: Eidsvold, no date (holotype ♀, paratype ♀ SPHTM), T. L. Bancroft, (paratypes, 1 ♂, SPHTM, 1 ♂, 1♀, CSIRO), no collector's name; Burnett River (paratypes, 1 ♂, 1 ♀, BM), T. L. Bancroft. New South Wales: Moree, October, 1951 (1 ♂, CSIRO), A. L. Dyce.

Cairnsimyia uniseta sp. nov.

(Figs 5, 18)

♂ : Head yellowish-brown variably suffused with darker brown; occipital and postgenal regions very pale; a large blackish blotch on ocellars and a pair of smaller ones surrounding the fronto-orbitals. Thoracic pleura light yellowish with brownish-yellow longitudinal markings; mesonotum reddish-brown with a variable pattern of yellowish-grey markings; scutellum yellowish with a pair of brownish spots towards the base. Legs yellowish-brown; femora often darker brown, especially on apical part; tibiae with a broad black apical band, a slightly narrower band before the middle and a very narrow basal band. Abdomen yellowish-brown, the tergites often slightly darker laterally.

Wing whitish-hyaline with brown spots more numerous and crowded than in *C. cavifrons*, three or four spots in costal cell; veins brown, not much paler basally.

Head structurally similar to that of *C. cavifrons;* one fronto-orbital; postverticals present but very small. Arista with numerous minute dark hairs which are much shorter than its basal diameter.

Thorax with prescutellar acrostichals well developed; scutellum with apical bristles closer to each other than to lateral bristles; propleuron with fine erect hairs in centre, propleural represented by a rather weak black bristle; mesopleuron with

numerous, long, black hairs, sometimes one of those near posterior margin slightly thickened and bristle-like. Femora without thickened ventral bristles or spines. Wing with vein 2 diverging from vein 3 at apex.

Tergite 6 free, both spiracles of sixth and seventh pairs present below its lateral edges. Hypopygium rather small; surstyli spatulate, slightly curved, about three times as long as greatest width; parameres small and narrow, with up to about seven terminal claw-like spines; no additional appendages present. Cerci separate with rather short hairs.

Dimensions: total length 4.5–5.2 mm; length of thorax 2.2–2.7 mm; length of wing 5.0–5.7 mm.

Distribution: southeastern Queensland; eastern New South Wales; Victoria.

Material examined—New South Wales: Kurrajong, 30th October, 1958 (holotype ♂, AM) D. K. McAlpine; 20 miles northwest of Upper Colo, November, 1955 (paratypes, 3 ♂, CSIRO), T. G. Campbell. Victoria: Warburton, January, 1924 (1 ♂, SPHTM), F. E. Wilson. Queensland: Brisbane, November, 1913 (1 ♂, UQ), H. Hacker, August, 1931 (1 ♂, UQ), F. A. Perkins.

Habitat: holotype on trunk of *Angophora costata* in dry sclerophyll forest.

Cairnsimyia cavifrons Malloch

(Fig. 19)

Malloch, 1931: 294–295, figs 1, 2.

McAlpine, 1958: fig. (as *Cairnsimyia* sp.).

Malloch's description is adequate for identification but the following points may be added:

Wing veins deep brown on entire distal part of wing and as far basad as primary forks of Rs (veins 2 and 3) and M (veins 4 and 5), basad of this level both veins and membrane conspicuously yellow.

Presutural bristles present but very small in all available specimens (absent in other species of the genus); mesopleuron with one to four outstanding setulae near posterior margin.

Surstyli about one and a half times as long as wide, dilated and slightly bilobed distally, the anterior lobe with fine hair-like setulae, the posterior one with short spine-like setulae on inner surface; lobes of hypandrium furnished with thickened setulae apically on inner surface; parameres appressed to inner basal surface of these lobes and thus not visible in lateral view, somewhat similar in form to those of *C. uniseta*. Aedeagus with a pair of unequally sclerotized longitudinal strips in basal part, the membranous distal part with a large irregular sclerite. Cerci very small and approximated but not completely fused.

♀: postabdomen normal, telescopic, with rather long, slender cerci.

Distribution: Queensland; northeastern New South Wales.

Material examined—Queensland: Cairns, 1907 (paratype ♂, AM), ex coll. B. Lichtwardt; Kuranda, September, 1910 (1 ♂, 1 ♀, BM, 1 ♂, AM), ex coll. E. A. Brunetti. New South Wales: Ulong, East Dorrigo district, no date (1 ♀, AM), W. Heron.

Other material (not seen by author): Cairns (holotype ♂, DEI), Kuranda (allotype and paratype, DEI), all ex Lichtwardt's collection.

It is suggested that both Lichtwardt's and Brunetti's material was probably collected by F. P. Dodd, who resided at Kuranda and sold insect specimens to collectors in many countries.

Cairnsimyia crosskeyi sp. nov.

(Figs 6, 20)

♂ ♀ : Head and thorax yellowish, with reddish-brown markings. Head with a large jet-black spot between each antenna and eye, and a smaller brown-black spot below it; a brown-black patch enclosing the postverticals and ocelli; a brown-black spot on each side enclosing the inner and outer verticals and another surrounding the fronto-orbital; a large brown area covering most of anterior part of frons; face and cheeks with extensive tawny markings; antennae deep yellowish, third segment brownish dorsally; arista dark-brown, paler basally; palpi yellowish-brown; proboscis dark-brown. Scutellum dull yellowish dorsally with small tawny marks, brown-black ventrally and at bases of apical bristles. Legs yellow-brown, the femora suffused with darker brown; tibiae with two dark-brown transverse bands, one sub-basal and one apical; tarsi strongly browned distally. Wing yellowish along anterior margin, extensively spotted with brown as in fig. 6. Abdomen brownish, tergites 2–5 with whitish dusting medially, most extensive on tergite 5.

Height of head slightly less than twice the length at level of antennae; the following bristles well developed: vibrissae, one fronto-orbital, inner and outer vertical cruciate postverticals, ocellar, a series of somewhat finer cheek bristles behind vibrissa; occiput with fine hairs from which the postocular setulae are not clearly differentiated. Third antennal segment horizontally ovoid; arista filiform, apparently bare, but with sparse minute hairs visible at a magnification of x100.

Mesoscutum without prescutellar acrostichal and presutural bristles; scutellum subtriangular, the apical pair of bristles closely placed; propleuron with fine pale hairs near centre, and a short propleural bristle below; mesopleuron with fine dark setulae in front, which become longer and stronger on posterior margin; one rather weak sternopleural bristle. Femora without thickened ventral bristles or spines; tibiae without preapical dorsal bristles.

Surstylus almost three times as long as maximum width, narrowed basally, truncate and slightly sinuate apically, with numerous setulae on most of surface; lateral lobe of hypandrium with numerous short setulae along posterior margin, some stout ones extending almost to apex on inner surface. Aedeagus somewhat similar to that of *C. cavifrons*, sclerite in distal part large and complex. Cerci minute, pubescent, without setulae.

♀ : postabdomen normal, retractile, with slender cerci.

Dimensions: total length, ♂ 4.3–6.0 mm, ♀ 4.5 mm; length of thorax, ♂ 2.5–3.3 mm. ♀ 3.0 mm; length of wing, ♂ 5.5–7.3 mm, ♀ 6.0–6.1 mm.

Distribution: Highlands of the Morobe District, New Guinea.

Material examined: Wau, 3,500–4,000 feet, 23rd May, 1965 (holotype ♂, BM, paratypes, 1 ♂, 1 ♀, BM, 1 ♂, AM, 1 ♀ CSIRO), R. W. Crosskey.

Habitat: specimens are labelled "At exudation on bark."

Cairnsimyia inscripta (Walker) new comb.

(Fig. 7)

Platystoma inscripta Walker, 1865: 120–121.

♂ ♀ : Very similar to *C. crosskeyi*. Costal and marginal cells without yellowish coloration. Arista somewhat thickened, except at extreme apex, basal segment brown, remainder white, clothed with dense white pubescence. Scutellum slightly narrower than in *C. crosskeyi*, both available specimens with three scutellar bristles on left side and two on right. Surstylus appears (on dry whole specimen) to be very like that of *C. crosskeyi* in form, and with similar hairing.

Distribution: West New Guinea—Dorey.

Material examined—New Guinea (1 ♂, 1 ♀, BM), A. R. Wallace. Compared with holotype by J. C. Deeming.

Other material (not seen by author): New Guinea (holotype, BM), ex W. W. Saunders' collection, examined for the author by J. C. Deeming. Walker (1868) indicates that this species was discovered by A. R. Wallace in New Guinea. Hence it is apparent that all specimens of the species here recorded must have been collected at Dorey, the only locality in New Guinea where Wallace collected.

Cairnsimyia aroana sp. nov.

(Figs 8, 12, 21)

♂ ♀: Head yellowish with reddish-brown markings on frons, face, and cheeks; a dark-brown spot surrounding each posterior fronto-orbital bristle, one surrounding inner and outer verticles, and one surrounding both postverticals and extending forwards to include the ocelli; a black spot between each antenna and eye; antennae deep yellowish, third segment slightly browned distally, arista black beyond base; palpi brownish-yellow; proboscis dark-brown. Thorax reddish-brown with extensive yellowish markings, the reddish-brown ground-colour partly obscured by pale blue-grey tomentum on pleura and sides of mesoscutum; scutellum whitish at apex. Legs brownish-yellow; tibiae with a broad brown apical transverse band and a rather obscure sub-basal one; tarsi brown, slightly paler basally. Wing with complex pattern of brown spots as in fig. 8. Abdominal tergites reddish-brown, paler at lateral margins; tergite 2 with large grey median patch; tergites 3–6 each with a pair of grey spots.

Height of head slightly more than (♂) or slightly less than (♀) twice the length at level of antennae; frons with a small pit or depression in front of anterior ocellus, a short transverse carina in front of this, below which the frons drops away vertically to ptilinal fissure; posterior fronto-orbital short and weak, anterior fronto-orbital very small or more frequently absent; outer verticals rather short and thick; inner verticals much shorter and thinner; postverticals moderately developed, incurved; ocellars usually indistinguishable; vibrissa no stronger than the anterior cheek bristles; postocular setulae short and fine above, thickened and spine-like below. Antenna as described for *C. crosskeyi*. Prelabrum with median process in male, which is reduced to little more than a prominence in female.

Thorax with humeral bristle absent (present in all other species of genus); prescutellar acrostichal and presutural bristles also absent; dorsocentral rather weak; scutellum transverse at apex, the apical bristles moderately close together; propleuron with numerous long pale hairs near centre, the propleural bristle pale and hair-like; most setulae on mesopleuron pale, hair-like, those near posterior margin blackish but not notably enlarged; sternopleural bristle small and weak. Femora without ventral spines; tibiae without preapical dorsal bristles.

Surstylus broadly triangular, very narrow at base, with a slight tooth or prominence on posterior margin; hypandrium with a comb of strong incurved setulae posteriorly near base on each side, its lobes with a few very short setulae on their inner surfaces, which do not extend to apices; aedeagus well sclerotized in both basal and distal sections; cerci minute, setulose, fused.

Female postabdomen as described for *C. crosskeyi*.

Dimensions: total length, ♂ 5.3–6.3 mm, ♀ 4.8–4.9 mm; length of thorax, ♂ 3.4–4.0 mm, ♀ 3.2 mm; length of wing, ♂ 6.3–7.5 mm, ♀ 5.6–6.1 mm.

Distribution: Papua—lowlands of the Central District.

Material examined: Aroana Estate, Aroa River, 6th December, 1963 (holotype ♂, paratypes, 3 ♂, 2 ♀, AM, paratype ♂, BM), D. K. McAlpine.

Habitat: all specimens taken at exuding sap of damaged tree (apparently *Ficus* sp.) in forest remnant.

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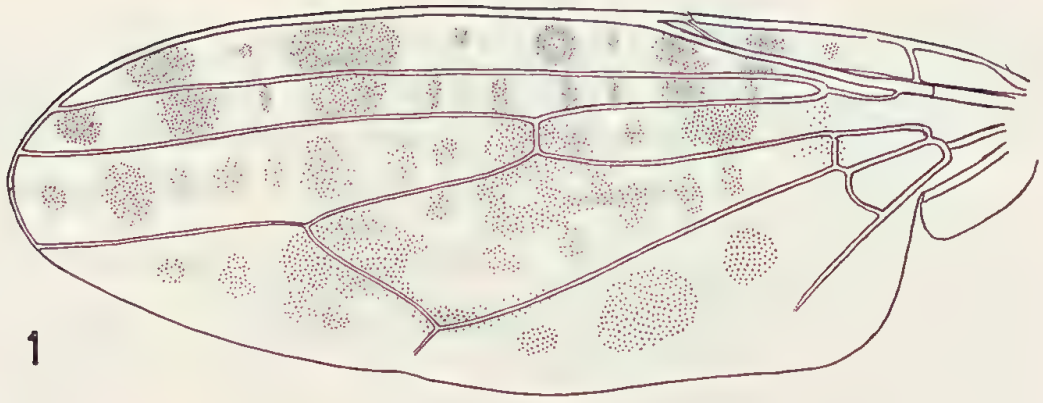
EXPLANATION OF FIGURES

1. *Cairnsimyia robusta*, wing, Kurrajong, New South Wales.
2. *C. sydneiensis*, wing of holotype.
3. *C. excavata*, wing of holotype
4. *C. verticalis*, wing of holotype.
5. *C. uniseta*, wing of holotype.
6. *C. crosskeyi*, wing of holotype.
7. *C. inscripta*, wing.
8. *C. aroana*, wing of holotype.
9. *Neorhinotora mutica*, diagram of protandrium.
10. *Rhinotora pluricellata*, diagram of protandrium.
11. *Cairnsimyia robusta*, diagram of protandrium.
12. *C. aroana*, head of holotype.
13. *C. sydneiensis*, head of holotype.
14. *C. robusta*, Hornsby, New South Wales. A, epandrium. B, hypandrium (aedeagus not shown.) C, inner aspect of right posterior paramere.
15. *C. excavata*, paratype. A, epandrium, B, hypandrium.
16. *C. sydneiensis*, paratype, Sydney, New South Wales. A, epandruim. B, hypandruim.
17. *C. verticalis*, genital segment of paratype, Eidsvold, Queensland.
18. *C. uniseta*, genital segment of paratype, Brisbane, Queensland.
19. *C. cavifrons*, Kuranda, Queensland. A, epandrium. B, left surstylus, posterolateral aspect (i.e., viewed at right angles to plane of surface). C, ejaculatory apodeme. D, hypandrium. E, right paramere, inner aspect.
20. *C. crosskeyi*, paratype. A, epandrium. B, hypandrium (aedeagus not shown).
21. *C. aroana*, paratype. A, epandrium. B, hypandrium.
22. *C. robusta*, last instar larva.
23. Cephalopharyngeal skeleton of same.
24. Facial region of same.
25. Left anterior spiracle of same.
26. Left posterior spiracle of same.

Note.—Unless otherwise stated, figures of genitalia are from the left lateral aspect. Setulae on tergite 9 have been omitted from some figures. a, aedeagus. ap, anterior paramere. b, ventral sclerotized band. c, cercus. pp, posterior paramere. s6–s9, sternites 6–9. sp, spiracle. ss, surstylus. t6–t9, tergites 6–9.

V. C. N. Blight, Government Printer, New South Wales—1963



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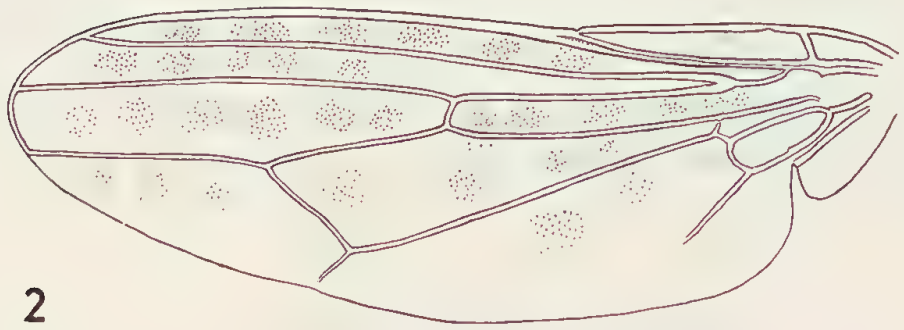

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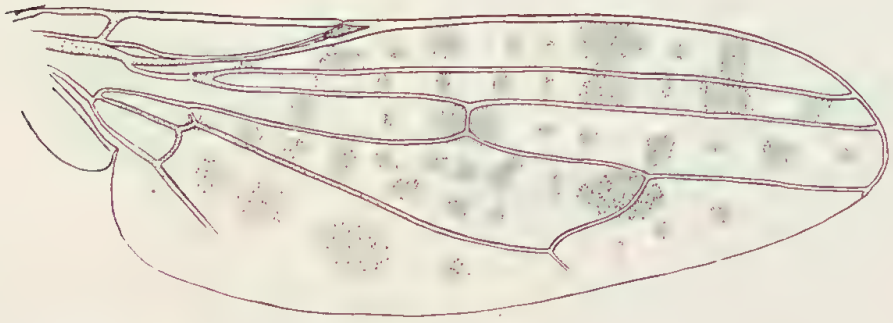

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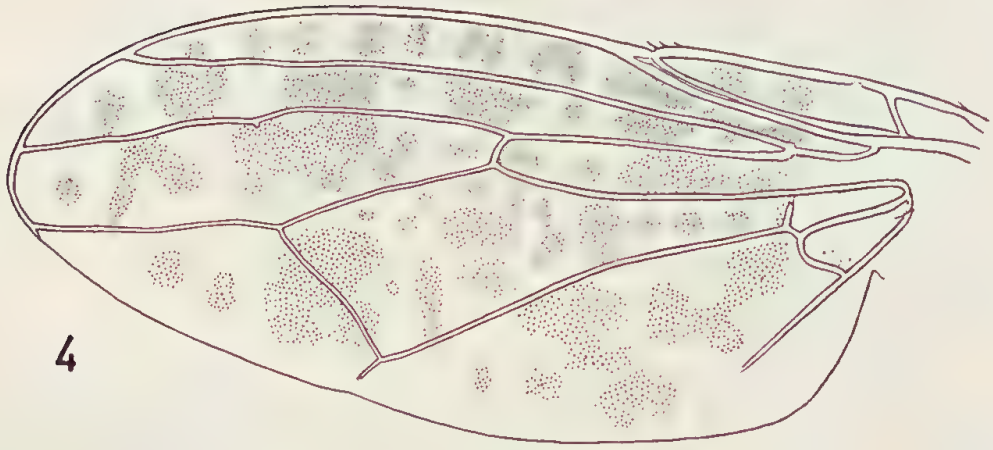

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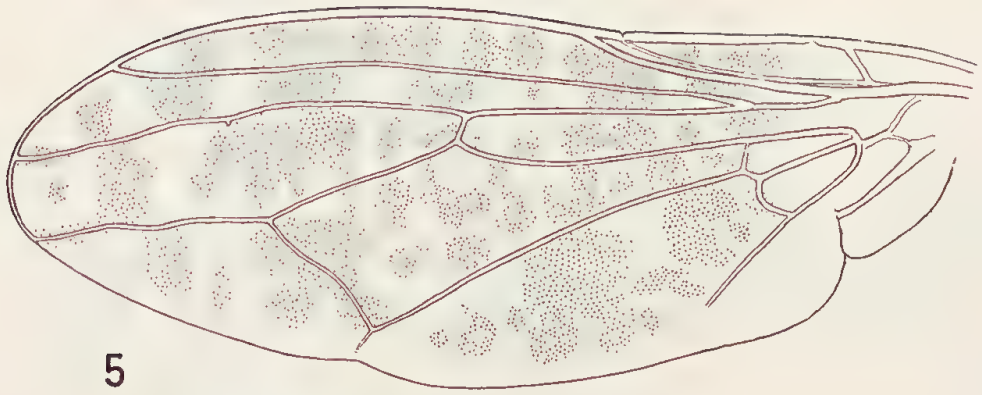
Figs 1–4



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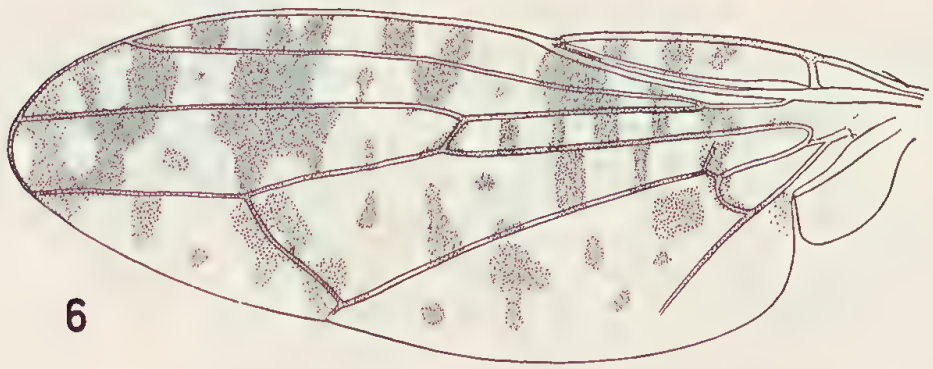

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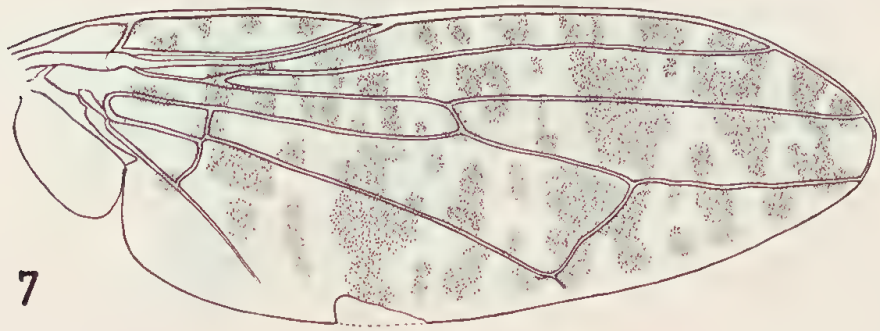

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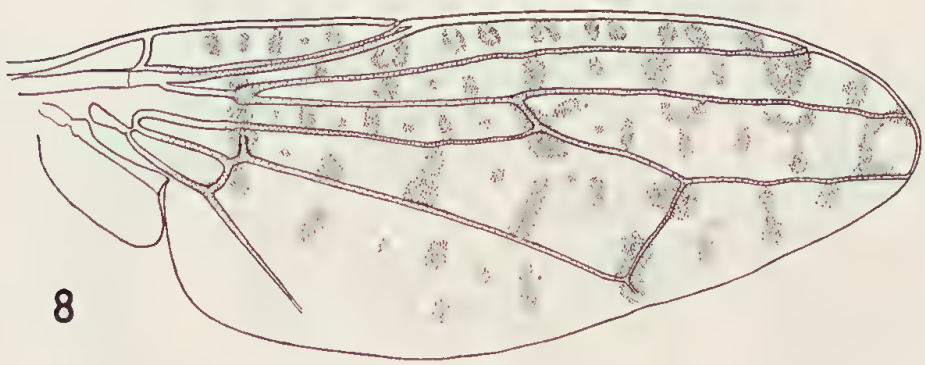

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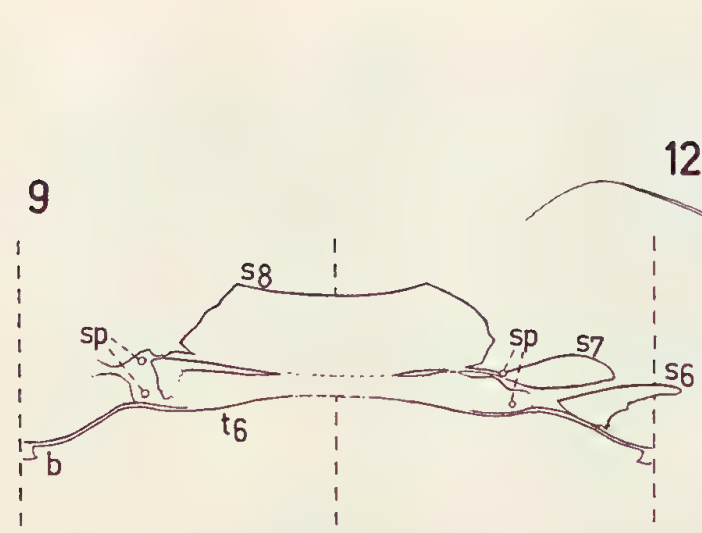
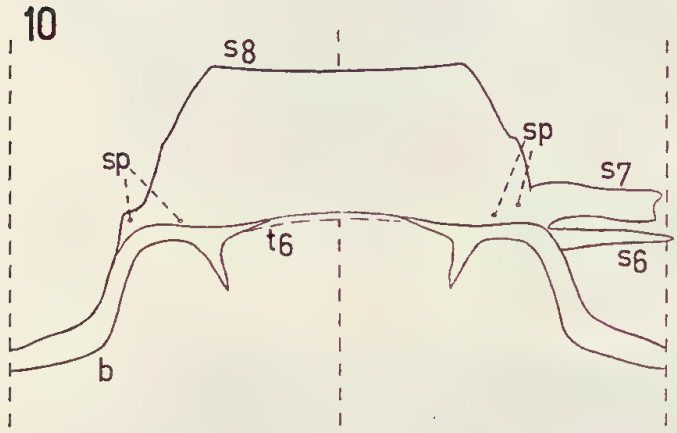
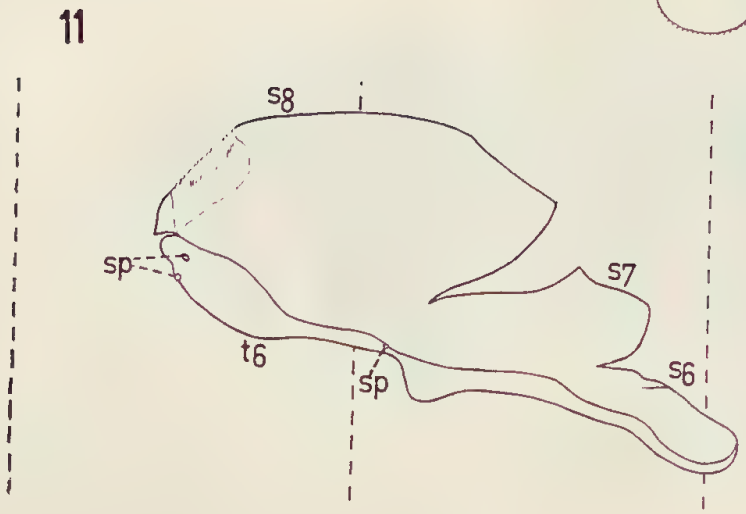
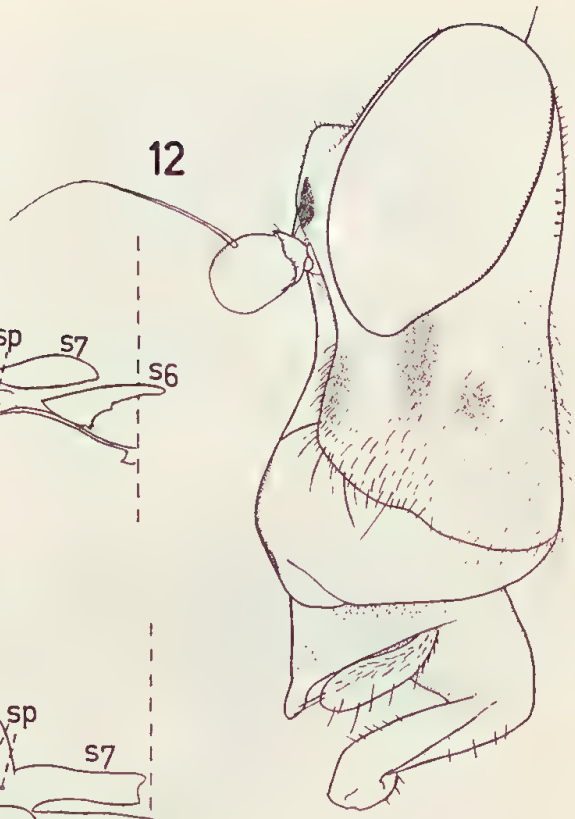
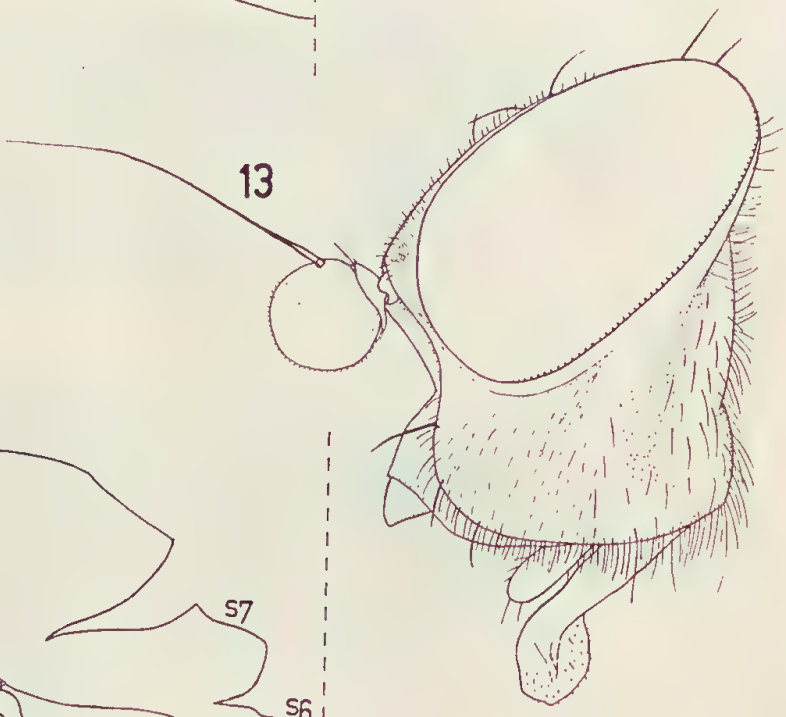
Figs 5–8



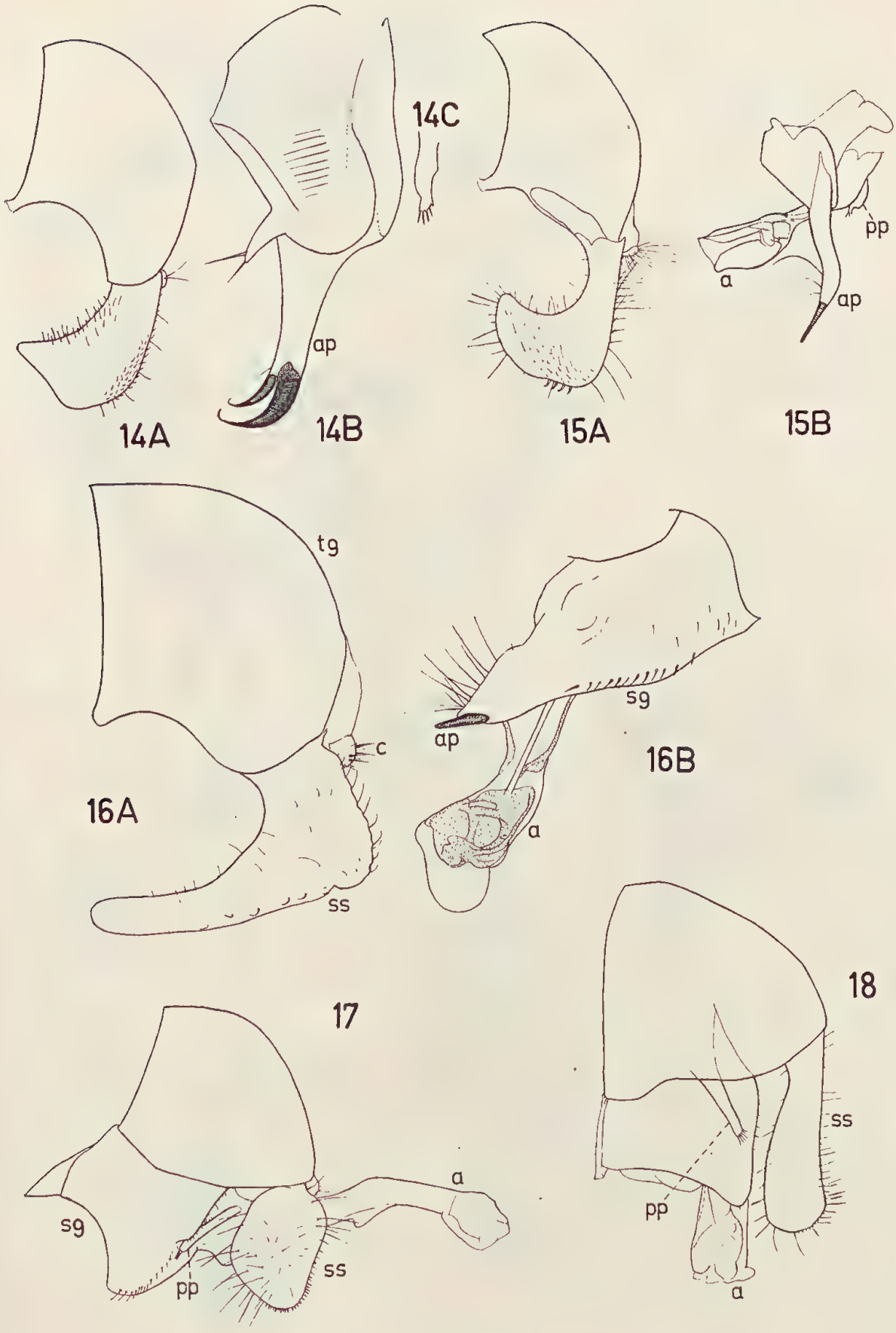








Figs 9–13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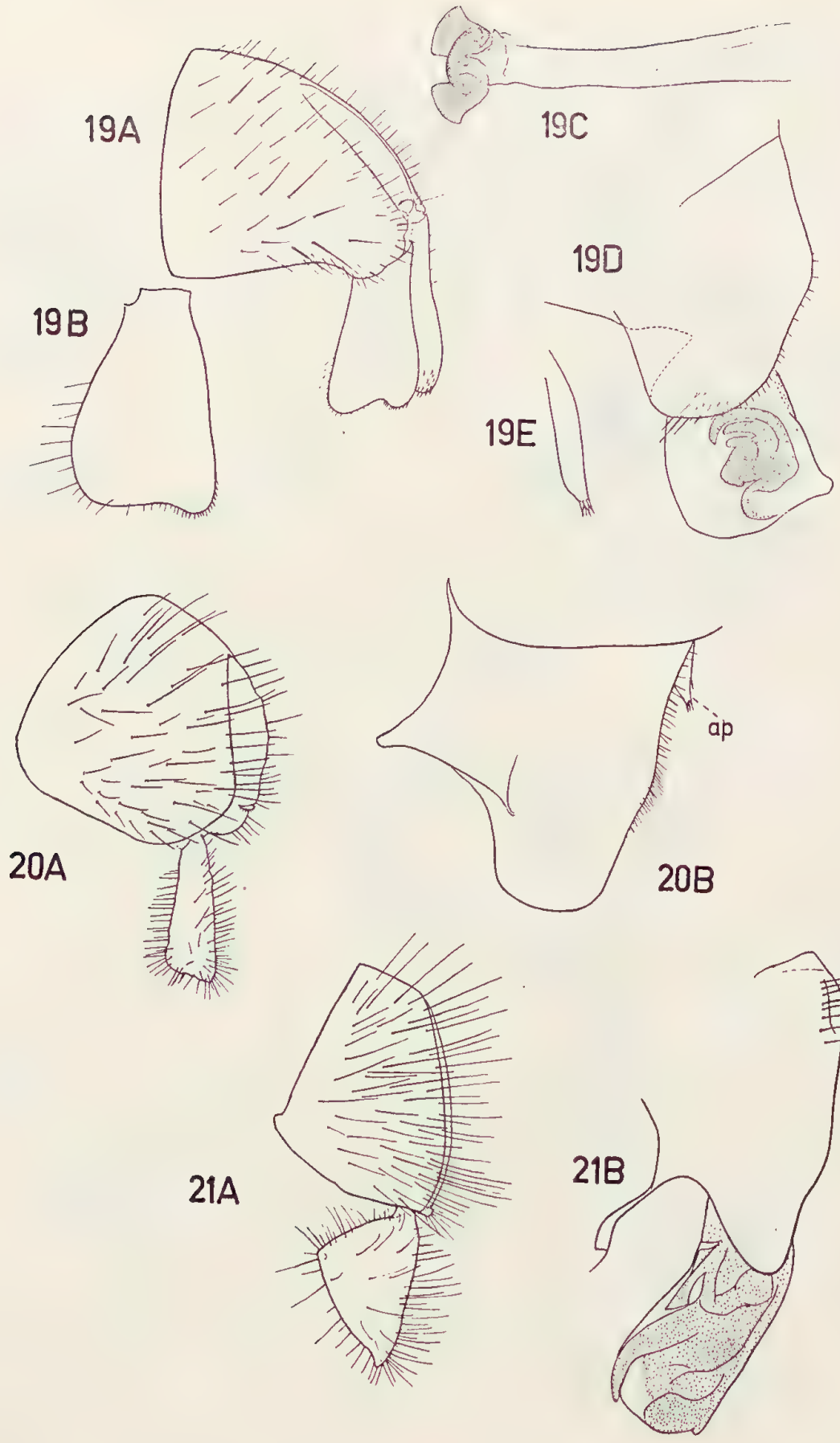
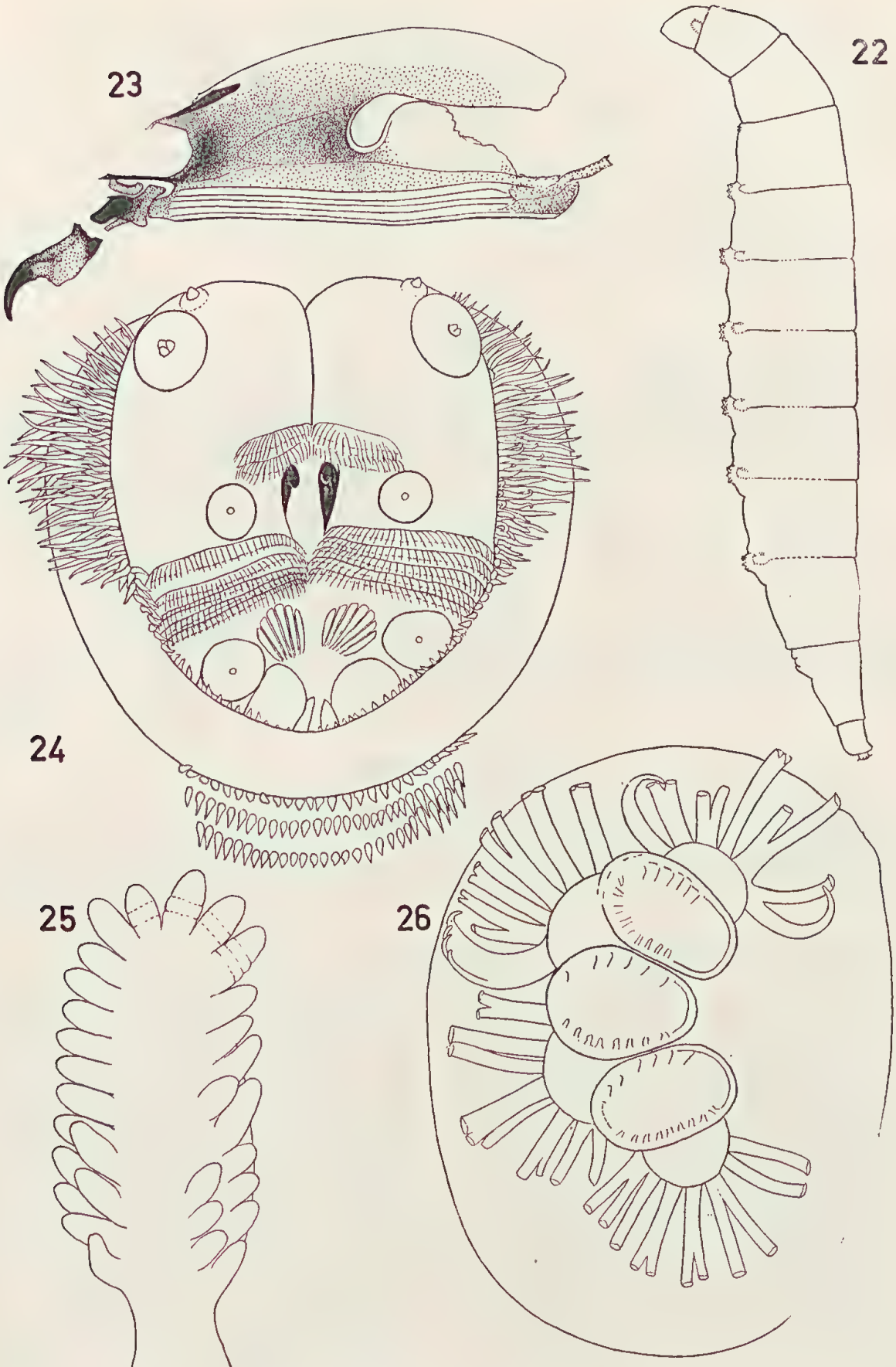
Figs 14–18



Figs 19–21



Figs 22–26

The *Endeavour* and Other Australian Museum Collections of Portunid Crabs (Crustacea, Decapoda, Portunidae)

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Plate 43. Figure 1.

Manuscript received, 26th September, 1967

SUMMARY

Portunids collected in 1909–1914 by the Fishery Investigation Ship *Endeavour*, held in the Australian Museum and not previously reported upon, are listed. Additional material collected by the *Endeavour* and held in the Mortensen collection, Zoologiske Museum, Copenhagen, is also listed. Specimens include a new State record of *Nectocarcinus spinifrons* Stephenson.

Two new species of *Caphyra* are described, *C. curtipes* n.sp. and *C. holocarinata* n.sp., and a third species is recognized as new, *C. carinata* nom. nov. Colour notes are given on *Charybdis yaldwyni*.

Caphyra unidentata is added to the Australian fauna, and new State records are given for *Macropipus corrugatus*, *Caphyra yookadai*, *Portunus pseudoargentatus*, *Thalamita crenata*, and *T. parvidens*. The distributions of *Charybdis truncata* and *Portunus orbitosinus* on the eastern Australian coast are extended. *Portunus gladiator* is recorded from Ceylon.

INTRODUCTION

This paper has two main aims: (a) completion of the recording of portunids collected by the Fishery Investigation Ship *Endeavour* and (b) the recording of interesting additions to the collections of the Australian Museum. For the sake of completeness two interesting specimens in the collections of the Queensland Museum are also included.

The majority of the portunids collected by the F.I.S. *Endeavour* during the years 1909–1914 and held by the Australian Museum have been reported upon by Rathbun (1923). Most of the remainder had been available to her and bore her preliminary identifications, although they were not referred to by her or by later workers (Stephenson and Hudson, 1957; Stephenson, Hudson, and Campbell, 1957; Stephenson and Campbell, 1959, 1960; Stephenson, 1961; Rees and Stephenson, 1966). Through the kindness of Dr D. J. G. Griffin, some additional *Endeavour* material held by the Zoologiske Museum, Copenhagen, and now under study by him with the Australian Brachyura collected by Dr Th. Mortensen and by the *Galathea* Expedition, has been made available to us. This remaining *Endeavour* material is reported on in the present work and in Stephenson and Rees (1968). These studies now hopefully complete the reporting of the *Endeavour* portunids. The status of *Charybdis incisa* Rathbun, 1923, from the *Endeavour* collections, is discussed by Stephenson, Hudson, and Campbell (1957, p. 502) and by Rees and Stephenson (1966, pp. 31–2), but Rathbun's other records from the 1923 report (with the exception of a *Nectocarcinus* specimen discussed below) stand unaltered. Included in the *Endeavour* collections is an interesting new record of another species of *Nectocarcinus* *N. spinifrons* Stephenson.

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Most of the recent additional specimens in the collections of the Australian Museum do not add substantially to the known distribution of species, and this material is not referred to here. Exceptions are the extension of the distributions of *Caphyra yookadai* Sakai, *C. unidentata* Lenz, *Thalamita crenata* (Latreille), and *T. parvidens* (Rathbun) to New South Wales, of *Macropipus corrugatus* (Pennant) to Queensland, and of *Portunus pseudoargentatus* Stephenson to the Northern Territory; a second record of *Portunus orbitosinus* Rathbun from Queensland; and a new record of *Charybdis truncata* (Fabricius) from Moreton Bay. Two new species are described, *Caphyra curtipes* n.sp. and *C. holocarinata* n.sp., and a new *Caphyra* is named, *C. carinata* nom. nov. Colour notes are given on the recently described species *Charybdis yaldwyni* Rees and Stephenson.

Two specimens of *Caphyra unidentata* Lenz held by the Queensland Museum are included in the present work because they were collected with two species of *Caphyra* which were sent to the Australian Museum.

The order of presentation follows Stephenson (1961). Dimensions given are carapace breadths in mm to the nearest 0.5 mm, as measured by dial calipers. The letters and numbers accompanying some specimens listed (e.g., P. 13726) are Australian Museum registered numbers, and the numbers prefixed by E (e.g., E. 715) refer to *Endeavour* material in the Australian Museum.

RECORDS AND DESCRIPTIONS OF SPECIES

Subfamily **CARCININAE** Alcock

Genus **Nectocarcinus** A. Milne Edwards

Nectocarcinus spinifrons Stephenson

Nectocarcinus spinifrons Stephenson, 1961, pp. 92–3, 95, figs 1A, 2G; pl. 1, fig. 1; pl. 4A.

Material examined: ♂ (32 mm), N. x W. of Greenly I., South Australia, 44 fm, E. 4511.

Distribution: The present specimen is the second recording of this species. Previously known only from Shark Bay, Western Australia, now extended to South Australia.

Nectocarcinus tuberculosus A. Milne Edwards

Nectocarcinus tuberculosus A. Milne Edwards, 1860, p. 220; 1861, pp. 405–6; pl. 37. Miers, 1874, p. 2. Haswell, 1882, p. 82. Hale, 1927, p. 153, fig. 154. Stephenson and Campbell, 1960, p. 84, fig. 2C; pl. 1, fig. 3; pls. 5C, 6B.

Material examined: ♂ (41 mm), off mouth of Murray River, South Australia, 20 fm, 17th August, 1909, E. 715. Juv. ?♂ (9 mm), Oyster Bay, Tasmania, 26 fm, P. 15184 (ex. E. 5185).

Remarks: The single *Endeavour* specimen without locality (♂, 11.6 mm, E. 6493) recorded as *Nectocarcinus integrifrons* (Latreille) by Rathbun (1923, p. 130) has been re-identified by us as *N. tuberculosus*.

Distribution: Victoria, Tasmania, and South Australia.

Subfamily **MACROPIPINAE** Stephenson and Campbell

Genus **Macropipus** Prestandrea

Macropipus corrugatus (Pennant)

Cancer corrugatus Pennant, 1777, p. 5; pl. 5, fig. 9.

Macropipus corrugatus (Pennant). Stephenson and Campbell, 1960, pp. 92–4, figs 1E, 2G; pl. 2, fig. 4; pl. 5G. Rees and Stephenson, 1966, p. 30.

Material examined: 8 juvs (6.5–7 mm), Oyster Bay, Tasmania, 26 fm, E. 5185. ♀ (10.5 mm), Bay of Fires, Tasmania, 53 fm, E. 6162. 16 ♂♂, 5 ♀♀ (11.5–17.5 mm), Disaster Bay, N.S.W., 30–40 fm, sand, mud, trawled, 1st October, 1914, Dr Th. Mortensen, *Endeavour*. 3 ♂♂ (24.5–29.5 mm), outside Moreton Bay, N. of Cape Moreton, South Queensland, trawled 20 fm, coll. trawler fishermen, September, 1966, P. 15379.

Distribution: New record for Queensland and northerly extension of known Australian distribution. Previously known from eastern northern Atlantic, Red Sea, Japan, Western Australia, and southeastern States of Australia (see Stephenson and Campbell, 1960).

In recent months considerable numbers have been obtained from prawn trawlers working in 60–90 fm off the south Queensland coast.

Subfamily **CAPHYRINAE** Alcock

Genus **Caphyra** Guérin

Caphyra curtipes n.sp.

Pl. 43A; figs 1A–D

? *Caphyra rotundifrons* (A. Milne Edwards). Barnard, 1957, pp. 2–3, fig. 1 (specimen A only).

Material examined: Holotype ♂ (11 mm), Woody Head, Clarence River mouth, N.S.W., from intertidal brown soft coral (*Alcyonium aspiculatum* Tixier-Durivault), A. A. Cameron and D. Cameron, 12th November, 1966, P. 15361.

Description:

Front—Bilobed, with the left side somewhat protruding, indistinctly subdivided into smaller median and broader lateral lobes, latter distinct from a reasonably sharp inner orbital lobe. Right side of front sinuous and merging with inner orbital lobe almost suggesting a malformation.

Anterolateral teeth—Anterolateral margin forming a ledge, clearly subdivided into three broad flat teeth, these being followed by fourth smaller, sharper tooth at end of epibranchial ridges.

Carapace—Broader than long (L/B 0.86), convex with flattened anterolateral margins. Granules on carapace anterior to ridges and just behind anterolateral teeth; remainder smooth and shiny. Mesogastric ridge continuous, slightly sinuous, concave anteriorly in midline. Pair of short sinuous ridges lateral to and slightly posterior to mesogastric. Epibranchials well developed.

Chelipeds—Right larger than left. General upper surfaces microscopically granular. Arm—anterior border with fine smooth continuous ridge, under surface smooth and shining. Wrist—with short, blunt, inner spine; upper surface with two short carinae, one running to inner spine, and one to hand articulation; outer surface with upper and lower carinae. Hand—slightly swollen; blunt tubercle at

wrist articulation; upper surface with two parallel carinae; remaining surfaces smooth and rounded. Fingers—short, stout; movable finger with two carinae on upper surface.

Legs—Elongate, slender. Dactyls short, with fringe of hairs on inner side. Propodi long.

Fifth legs—Curved back dorsally over carapace. Propodus broad (L/B 2.05), fringed anteriorly with a few hairs. Dactyl narrow and very sharp tipped.

Male abdomen—Penultimate segment broader than long (L/B 0.7), with slightly converging borders. Ultimate segment triangular, about as broad as long.

Male first pleopods—Almost straight, except for sharp change in curvature near tip, where it tapers to a point. Apart from a few scattered hairs on basal lobes, appendage bare to terminal armature. Inner side bears long irregular row of fairly stout bristles terminating just before tip. Outer side bare except for a small cluster of bristles at tip. Upper surface with dense patch of bristles near tip, merging with those of inner side.

Colour—When first examined, about 3 months after collection, the anterior half of the carapace had faint longitudinal bars of pigment. These have since faded.

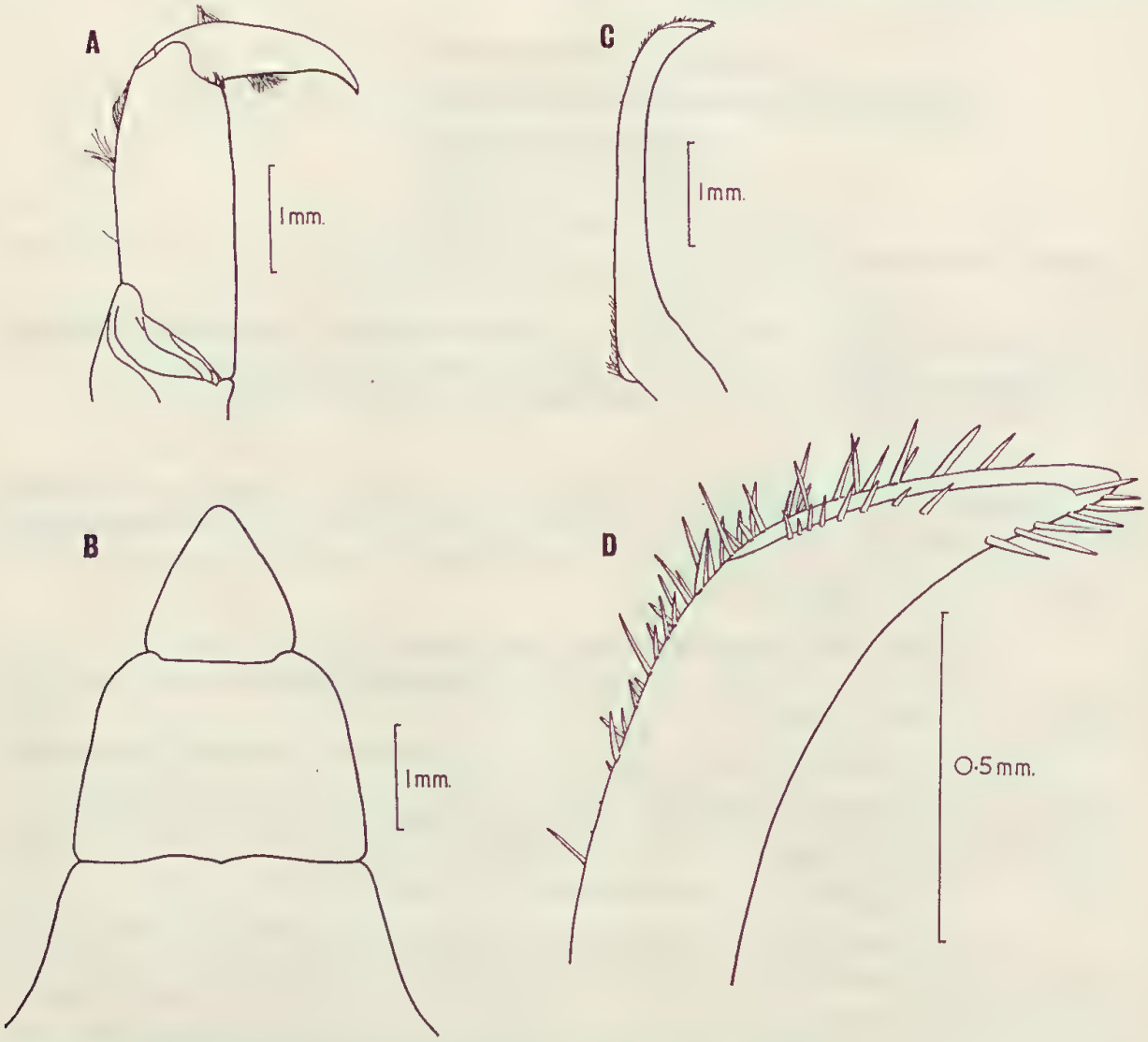

Fig. 1.—*Caphyra curtipes* n. sp. A, dactyl and propodus of right fifth leg; B, male abdomen; C, right male first pleopod; D, tip of pleopod.

Remarks:

This species keys out in Stephenson and Campbell (1960, pp. 96–7) with *C. alcyoniophila* Monod, but differs from it in the shape of the front, in the shape of the anterolateral teeth, in the broader propodus of the fifth leg, in the shape of the male abdomen, and in the less dense terminal armature of the male first pleopod.

Barnard (1957, pp. 2–3, fig. 1) records *C. rotundifrons* (A. Milne Edwards) from South Africa and figures two specimens. As indicated below under *C. yookadai* these are neither *C. rotundifrons* (A. Milne Edwards) nor *C. yookadai* Sakai. Barnard's figures and description of specimens B and C show a feebly developed inner supraorbital lobe, two very obtuse anterolateral teeth and a last walking leg with very broad propodus. In this last respect it shows resemblances to the present species although the shape of the propodus is distinctly different. Barnard's description and figures of his specimen A show a front, inner supraorbital angle and anterolateral teeth resembling the present species. It appears to belong to a different species from his specimens B and C, and until it is redescribed its status must remain uncertain.

In company with *C. curtipes*, and apparently from the same alcyonarian host (*Alcyonium aspiculatum*), *C. unidentata*, and *C. yookadai* are recorded (see later). This adds credence to the suggestion that Barnard's material, also all from a single host, comprises more than one species.

Caphyra holocarinata n.sp.

Pl. 43B

Material examined: Holotype. ♀ (10 mm), reef near Kunie, Port of Kuto, Isle of Pines, off New Caledonia, mid tide level, E. Pope, 19th July, 1960, P. 13726.

Description:

Front—Indistinctly six lobed; median and submedian almost fused to a broad sinuous lobe; laterals rounded. Inner orbital lobes rounded, clearly separated from and less protruding than frontal lobes.

Anterolateral teeth—Four, stout; first three moderately blunt, last the narrowest and sharpest.

Carapace—Convex, broader than long (L/B 0.6), shiny, finely granular in anterior half. Epibranchial ridge well developed, backwardly directed. No other carapace ridges.

Chelipeds—Right larger than left. Arm—anterior border with three small blunt, flattened spines; under surface smooth. Wrist—microscopically granular, with short, stout, blunt inner spine. Hand—rounded tubercle at wrist articulation, single uninterrupted carina on upper inner surface of hand. Fingers—short, stout.

Legs—Elongate, slender. Dactyls short, with fringe of long hairs on inner side. Propodi long. Fifth legs missing.

Remarks:

This species is close to *C. laevis* (A. Milne Edwards), differing from it in having (a) smaller, less conspicuous and generally fewer spines on the anterior border of the arm; (b) shorter, blunter inner wrist spine; (c) absence of spine on carina of hand. The form of the front differs from *C. laevis* as shown by Crosnier (1962, fig. 43 *bis* a), but comes within the range of variation shown by Stephenson and Campbell (1960, fig. 3D–F). It is very similar to their fig. 3F.

C. holocarinata is distinguished from most specimens of *C. laevis* by possessing only four anterolateral teeth on each side instead of five. Occasional specimens of *C. laevis* do, however, possess four teeth as indicated by Haswell's (1882) description of a synonym of this species, *C. octodentata* (see Stephenson and Campbell, 1960, pp. 100–1; Rees and Stephenson, 1966, p. 30).

Caphyra laevis (A. Milne Edwards)

Goniosoma laeve A. Milne Edwards, 1869, p. 152.

Caphyra laevis (A. Milne Edwards). A. Milne Edwards, 1873, pp. 173–4; pl. 4, figs 2a–c. Stephenson and Campbell, 1960, pp. 97–8, 100–1, figs 1G, 2I, 3D–G, 3J; pl. 3, fig. 3; pl. 5I. Crosnier, 1962, pp. 32–4, fig. 43 *bis* a–b. Rees and Stephenson, 1966, p. 30.

Caphyra octodentata Haswell, 1882, pp. 753–4.

Material examined: ♀ (13 mm), West I., off Rockhampton, Queensland, E. 4510.

Distribution: Malgache (= Madagascar), Amboina, Australia (Queensland), New Caledonia, and Fiji.

Caphyra unidentata Lenz

Caphyra unidentata Lenz, 1910, pp. 555–6, figs. 2–4. Crosnier, 1962, pp. 28, 30, figs 33–8.

Material examined: ♂ (7 mm), Woody Head, mouth of Clarence River, N.S.W., from intertidal brown soft coral (*Alcyonium aspiculatum* Tixier-Durivault), A. A. Cameron, 7th January, 1966, P. 15378. ♂ (8.5 mm), ♀ (10 mm), Woody Head, mouth of Clarence River, N.S.W., on soft coral, A. A. Cameron, 10th December, 1966, Qld Mus. W. 2575.

Remarks:

As mentioned earlier, three species of *Caphyra*, *C. unidentata*, *C. yookadai*, and *C. curtipes*, were all collected from the one host, a brown soft coral.

The present species, not previously recorded from Australia, differs slightly from Crosnier's figures (figs 33–8). The 8.5 mm male possesses a more sinuous front, slightly broader ultimate segment of the male abdomen, and fewer bristles on the outer surface of the pleopod. These differences may be due to its juvenility.

The 7 mm male differs from Crosnier's figures (figs 33, 34) in possessing a distinctly bilobed front, and in the outer surface of hand of cheliped being granular. Crosnier mentions only "granules miniscules sur sa face supérieure."

Distribution: New record for Australia. Previously known only from Madagascar and Fiji.

Caphyra yookadai Sakai

Pl. 43, C

Caphyra yookadai Sakai, 1933, pp. 141–3, pl. 13, fig. 3. Stephenson and Campbell, 1960, pp. 102–4, figs 1I, 2K, 3H; pl. 4, fig. 1; pl. 5K. Stephenson, 1961, pp. 98–9; pl. 1, fig. 3. Rees and Stephenson, 1966, pp. 30–1.

Non *Caphyra yookadai* Crosnier, 1962, pp. 31–2, figs 40–43 (= *C. carinata* nom. nov.).

Material examined: ♀ (8.5 mm), Woody Head, Clarence River mouth, N.S.W., from intertidal brown soft coral (*Alcyonium aspiculatum* Tixier-Durivault), A. A. Cameron, Jan., 1966, P. 15373. Ovig. ♀ (9 mm), locality as above, 7th March, 1966, A. A. Cameron, P. 15374. ♀ (9 mm), locality as above, 23rd March, 1966, A. A. Cameron, P. 15375. ♂ (9.5 mm), ♀ (7 mm), locality as above, 20th September, 1966, A. A. Cameron, P. 15376. 3 ♂♂ (8.0–8.5 mm) 3 ovig. ♀♀ (8.0–10.5 mm), locality as above, 12th November, 1966, D. and A. A. Cameron, P. 15360.

Remarks:

One of the 8 mm males of P. 15360 has very indefinite anterolateral teeth and the intermediate sized female of P. 15360 has five anterolateral teeth on the left. Previously a range of 2–4 teeth had been reported by Stephenson and Campbell (1959, p. 103).

The colour of two specimens (♂, 9.5 mm; ♀, 7 mm) was pale cream with dark grey blotches, while the third (♀, 9 mm) bore an orange-tinged carapace with orange-brown spots. These differed from Sakai's (1939, pl. 18, fig. 4) with whitish-pink base and brown mottling, and from Stephenson's (1961, pl. 1, fig. 3) material which was "shiny white with pottery blue blotches".

Crosnier's (1962) description and figures differ in several respects from the present material and from that previously recorded from Australia (Stephenson and Campbell, 1960; Stephenson, 1961). The most important differences are:

(a) front more salient and each side more clearly bilobed;

(b) a continuous and sinuous mesogastric ridge;

(c) outer surface of palm of cheliped distinctly carinate, fingers carinate;

(d) propodus of fourth walking leg relatively broad (from Crosnier's figure 42, c. 2.7 times as long as broad).

In these respects Crosnier's specimen also differs from Sakai's description, figures, and plate.

Crosnier's species has resemblances to both *C. alcyoniophila* Monod, 1928 and to *C. curtipes* but differs from the former in its broader carapace, more protruding front, and mesogastric carapace ridge. It differs from *C. curtipes* in its front, mesogastric carapace ridge and having a longer propodus on the last walking legs. It is almost certainly an undescribed species to which the name *C. carinata* nom. nov. is now given, because of the carination of the outside of the palm and finger.

The three species, *C. alcyoniophila*, *C. carinata*, and *C. curtipes*, key out together in Stephenson and Campbell (1960, pp. 96–7 couplet 7) but can be separated as follows:

a. Outer surface of palm of cheliped carinate ..... *C. carinata* nom. nov.

Outer surface of palm of cheliped not carinate ..... b

b(a). First anterolateral tooth the longest, male abdomen almost twice as broad as long ..... *C. alcyoniophila* Monod.

Third anterolateral tooth the longest, male abdomen about one and a third times as broad as long ..... *C. curtipes* n.sp.

Barnard's *C. rotundifrons* (A. Milne Edwards) was incorrectly synonymized with *C. yookadai* by Stephenson and Campbell (1960). It differs noticeably in the proportions of propodus of the fourth walking leg, which from Barnard's figure

appears to be approximately twice as long as broad. It is also evident from the shape of the front that Barnard's material does not belong to *C. rotundifrons* (A. Milne Edwards) and it is further discussed under *C. curtipes*.

Distribution: *C. yookadai* which was previously recorded in Australia only from Myora, Moreton Bay, Queensland, is now known from New South Wales. Also from Izu and Kii Peninsulas, Japan.

Subfamily **PORTUNINAE** Stephenson and Campbell

Genus **Lupocyclus** Adams and White

Lupocyclus rotundatus Adams and White

Lupocyclus rotundatus Adams and White, 1849, p. 47; pl. 12, fig. 4. Stephenson and Campbell, 1960, pp. 109–11, figs 1K, 2M; pl. 4, fig. 3; pl. 5M. Stephenson, 1961, pp. 102–3, fig. 3B.

Material examined: ♀ (36.5 mm), 7 miles NNE. of Bowen, Queensland, 16 fm, 3rd August, 1910, E. 3104.

Distribution: Ceylon, Andamans, Borneo, Amboina, Malay Peninsula, Japan, Western Australia, and nothern Queensland.

Genus **Charybdis** de Haan

Charybdis truncata (Fabricius)

Portunus truncata Fabricius, 1789, p. 365.

Charybdis (*Goniohellenus*) *truncata* (Fabricius). Stephenson, Hudson, and Campbell, 1957, pp. 503–4, figs 2D, 3E; pl. 3, fig. 3; pl. 4I. Rees and Stephenson, 1966, p. 39. Stephenson, 1967, p. 12.

Material examined: ♂ (35 mm), trawled 7 miles E. of Scarborough, Moreton Bay, Queensland, 7½ fm, sandy mud, 10th November, 1966, W. Stephenson and E. Jukkola. 31 ♂ ♂, 21 ♀ ♀, 18 ovig. ♀ ♀, 2 *Sacculina* infested specimens, trawled in 6 samples each 10 mins duration between Mud I. and sandhills on Moreton I., Moreton Bay, Queensland, 5½–18 fm, 19th December, 1966, W. Stephenson and E. Jukkola, P, 15385, 15386 (1 ♂, 1 ♀ only).

Distribution: Previously known in Queensland only from the North coast. Now known from India to Japan including eastern and western Australia.

Charybdis yaldwyni Rees and Stephenson

Charybdis (*Charybdis*) *yaldwyni* Rees and Stephenson, 1966, pp. 32–5; pl. 7C, fig. 1D–F.

Material examined: 7 ♀ ♀ (32.5–40 mm), 6 ovig. ♀ ♀ (39–43.5 mm), Tr. Sta. IV, 4 miles W. of small sand hill on Moreton I., Moreton Bay, Queensland, sandy mud, 10–12½ fm, 19th December, 1966, W. Stephenson and E. Jukkola.

Remarks:

Rees and Stephenson (1966) did not give colour notes on this species nor on the closely related *C. jaubertensis*. The specimens of *C. yaldwyni* from Moreton Bay bore the following pattern of dark red markings:

Carapace bearing a broad diffuse V extending from the protogastric ridges to the cardiac region. Epibranchial, mesobranchial, and posterior regions diffusely

pigmented. Concentrations of pigment on lateral ends of protogastric, mesogastric, and metagastric ridges, on cardiac region and median postcardiac region. Discrete spots present over all diffusely pigmented areas.

Frontal and anterolateral teeth, and postlateral borders reddish-orange.

Chelipeds diffusely purplish-red with scattered blood-red spots. Concentrations of pigment present on spines on anterior border of arm, inner wrist spine, upper inner spines on hand, and proximal portion of movable finger. Walking legs banded in brown and pale orange.

C. jaubertensis, as restricted by Rees and Stephenson (1966, pp. 32–7), differs from the present species in being generally less pigmented and bears a large conspicuous blood-red spot in each mesobranchial area.

Distribution: North Australia from Exmouth Gulf, Western Australia, to Moreton Bay, Queensland.

Genus **Portunus** Weber

Portunus gladiator (Alcock)

? *Portunus gladiator* Fabricius, 1798, p. 368.

Neptunus (Amphitrite) gladiator Alcock, 1899, pp. 33–6. Shen, 1937, pp. 101–3, figs 2a–c.

Portunus gladiator Crosnier, 1962, pp. 51–4, figs 72, 76, 78, 82–83; pl. 3, fig. 2. Stephenson and Rees, 1967a, pp. 24–5.

Material examined: ♂ (62 mm), ovig. ♀ (46.5 mm), Ceylon Pearl Banks Inspection, Moderagam Paar, 26th November, 1921, exch. Colombo Museum, Ceylon, P. 7680, P. 7681.

Remarks: See *P. pseudoargentatus*.

Distribution: East Coast of Africa, Ceylon.

Portunus gracilimanus (Stimpson)

Amphitrite gracilimanus Stimpson, 1858, p. 38; 1907, p. 77; pl. 10, fig. 3.

Portunus gracilimanus (Stimpson). Stephenson and Campbell, 1959, pp. 115–6, figs 2M, 3M; pl. 4, fig. 1; pls 4M, 5M. Stephenson, 1967, pp. 14–5.

Material examined: ♂ (c. 45 mm), 7 miles NNE. of Bowen, Queensland, 16 fm, 3rd August, 1910, E. 3105.

Distribution: Andamans, East coast of India, Malaysia, New Guinea, Australia (Northern Territory and Queensland), and Hong Kong. Recently two or three specimens have been trawled in Moreton Bay, southern Queensland, thus extending the distribution further south.

Portunus granulatus (H. Milne Edwards)

Lupea granulata H. Milne Edwards, 1834, p. 454.

Portunus granulatus (H. Milne Edwards). Stephenson and Campbell, 1959, pp. 108–10, figs 2I, 3I; pl. 3, fig. 1; pls 4I, 5I. Stephenson, 1961, p. 108. Stephenson and Rees, 1967a, pp. 25–7, fig. 5.

Material examined: Ovig. ♀ (21 mm), One Tree Island, Capricorn Group, Queensland, dredged from lagoon, 12–15 ft at L.W., J. C. Yaldwyn and Museum party, November, 1966, P. 15369.

Remarks: Dredged from the One Tree Island lagoon in association with *P. longispinosus* and *P. orbitosinus.*

Distribution: Madagascar and Red Sea to Hawaii, Samoa and Fiji, including Japan and Australia (western, northern and eastern, extending into New South Wales).

Portunus longispinosus Rathbun

? *Amphitrite longispinosa* Dana, 1852, pp. 277–8; pl. 17, fig. 2.

Portunus (Xiphonectes) longispinosus Rathbun, 1906, p. 871; pl. 12, fig. 6.

Material examined: ♀ (c. 25 mm), One Tree Island, Capricorn Group, Queensland, dredged from lagoon, 12–15 ft at L.W., J. C. Yaldwyn and Museum party, November, 1966, P. 15368.

Remarks:

This species belongs to the "*P. longispinosus* complex", and keys out as *P. longispinosus* (Dana) in Stephenson and Rees (1967, pp. 29–30).

However, the present specimen differs from Rathbun's (1906) pl. 12, fig. 6 in (a) its decidedly less embossed carapace, (b) the last anterolateral spine being directed laterally and not backwardly and (c) the spinous projections on the postlateral junctions being less conspicuous. In these features it more closely resembles Stephenson and Campbell's (1959) plate 2 fig. 2, although differing from it in the length of the last anterolateral spine.

It appears similar to *P.* cf. *longispinosus* Rathbun (see Stephenson and Rees, 1967, p. 30), in possessing a less strongly embossed carapace.

Distribution: Species of the "*P. longispinosus* complex" are known in the Australian areas from Western Australia, Queensland, and Lord Howe Island.

Portunus orbitosinus Rathbun

Portunus (Amphitrite) gladiator de Haan, 1833, p. 65; pl. 18, fig. 1.

Portunus (Achelous) orbitosinus Rathbun, 1911, p. 205; pl. 15, fig. 11.

Portunus orbitosinus Rathbun. Stephenson and Campbell, 1959, pp. 113–4, figs 2L, 3L; pl. 3, fig. 4; pls 4L, 5L. Stephenson, 1961, pp. 108–9; 1967, p. 17. Stephenson and Rees, 1967a, pp. 31–4, fig. 6.

Material examined: ♀ (c. 27 mm), Gillett Cay, Swain Reefs, Queensland, from sand flats at NE. end of Cay, Aust. Mus. Swain Reefs Exped., Oct., 1962, P. 15358. ♀ (23.5 mm), One Tree I., Capricorn Group, Queensland, dredged from lagoon, 12–15 ft at L.W., J. C. Yaldwyn and Museum party November, 1966, P. 15351.

Distribution: Second record from Queensland. Previously known from Madagascar, Seychelles, Western Australia, Mapoon (northern Queensland), and Japan.

Portunus pseudoargentatus Stephenson

? *Portunus gladiator* Fabricius, 1798, p. 368.

Portunus (Amphitrite) gladiator de Haan, 1835, p. 39; pl. 1, fig. 5.

Neptunus (Amphitrite) gladiator Sakai, 1939, pp. 390–1, fig. 5a; pl. 47, fig. 3.

Portunus pseudoargentatus Stephenson, 1961, pp. 109–11, figs 2A, 3F; pl. 2, fig. 4; pls 4F, 5D. Stephenson and Rees, 1967a, p. 25.

Material examined: ♀ (44.5 mm), Troubadour Reef, approx. 10° S., 129° E., edge of Sahul Shelf off Darwin, N.T., dip net on surface over 17 fm, G. P. Whitley, *Stanley Fowler* Exped., 6th September, 1949, P. 14193.

Remarks: The present specimen and the type of *P. pseudoargentatus* have blunter frontal teeth than a specimen of *P. gladiator* identified by Crosnier or the Ceylon specimens of *P. gladiator* (see p. 293).

Distribution: From the Philippines, Japan, northern and western Australia. Second known specimen from Australian waters.

Portunus rubromarginatus (Lanchester)

Achelous rubromarginatus Lanchester, 1900, pp. 746–7; pl. 46, fig. 8.

Portunus rubromarginatus (Lanchester). Stephenson and Campbell, 1959, pp. 112–3, fig. 2K, 3K; pl. 3, fig. 3; pls 4K, 5K. Stephenson and Rees, 1967a, p. 37. Stephenson, 1967, p. 18.

Material examined: 3 ♂♂ (47.5, 48.5, 51.5 mm), ♀ (44 mm), 4–5 miles SW. of Bustard Head, Queensland, 11–16 fm, 8th July, 1910, E. 2032, E. 2033, E. 2034, E. 2035. ♂ (63 mm), Platypus Bay, Hervey Bay, Queensland, 28th July, 1910, E. 3107. ♂ (59.5 mm), 7 miles NNE. of Bowen, Queensland, 16 fm, 3rd August, 1910, E. 3106.

Distribution: Malay Archipelago, South China Sea, Hong Kong, northern half of Australia (on the east coast, including Moreton Bay).

Genus **THALAMITA** Latreille

Thalamita crenata (Latreille)

Portunus crenatus Latreille, 1829, fide H. Milne Edwards, 1834.

Thalamita crenata (Latreille) H. Milne Edwards, 1834, p. 461. Stephenson and Hudson, 1957, pp. 332–4, figs 2Q, 3Q; pl. 2, fig. 3; pls 7F, 9C. Stephenson and Rees, 1967a, pp. 66–9.

Material examined: 2 ♂♂ (36 mm, 69 mm), lagoon, Lord Howe I., Miss Julie Booth, August, 1962, P. 14190, 14191. ♂ (15 mm), Bayview, Pittwater, Sydney, N.S.W., mangrove mud flat, Miss Patricia McDonald, 16th May, 1966, P. 15392.

Distribution: Now extended to New South Wales and Lord Howe I. Previously known from East Africa, Red Sea, Philippines, Japan, Society Islands, and the northern half of Australia.

Thalamita macropus Montgomery

Thalamita macropus Montgomery, 1931, pp. 431–2; pl. 24, fig. 4; pl. 28, fig. 2. Stephenson and Hudson, 1957, pp. 343–4, figs 2J, 3J; pl. 4, fig. 1; pls 7J, 10H. Stephenson, 1961, p. 122.

Material examined: 2 ♂♂ (10.5, 12 mm), ♀ (11 mm), 1 juv. (7 mm), 37° 05′ S., 150° 05′ E., off Twofold Bay, N.S.W., 30–50 fm, sand, "Dynd, Skraber", 30th September, 1914, Dr Th. Mortensen, *Endeavour*. ♂ (17.5 mm), 2 ♀♀ (11, 17.5 mm),

Disaster Bay, N.S.W., 30–40 fm, sand, mud, trawled, 1st October, 1914, Dr Th. Mortensen, *Endeavour*. Ovig. ♀ (16 mm), near Eden, N.S.W., 20–25 fm, "Blod Bd., Skraber", 1st October, 1914, Dr Th. Mortensen, *Endeavour*.

Remarks: The juvenile (7 mm) does not possess the subsidiary basal tooth on the first anterolateral tooth, but appears to agree in other respects with this species.

Distribution: Western Australia and New South Wales.

Thalamita parvidens (Rathbun)

Thalamonyx parvidens Rathbun, 1907, p. 62; pl. 5, fig. 9.

Thalamita parvidens (Rathbun). Sakai, 1939, pp. 425–6, fig. 19. Stephenson, 1961, pp. 122–4, figs 2F, 4B; pl. 4, fig. 1; pls 4K, 5H. Stephenson and Rees, 1967a, pp. 82–4, fig. 30.

Material examined: 2 ♂ ♂ (10 mm, 11 mm), trawled in Wallis Lake, near Forster, N.S.W., from shrimp net over mud bed, Univ. of N.S.W. party, 7th December, 1966, P. 15359.

Remarks:

The present specimens key out in Stephenson and Hudson (1957, p. 318) as *T. poissoni* (Audouin and Savigny) because the anterolateral teeth are more acute than could be expected due to their juvenility. Stephenson and Hudson's key needs alteration at couplet 46, because the present material, together with Sakai's (1939, fig. 19a), shows distinct mesobranchial ridges.

The larger specimen possesses a pleopod similar to that shown by Stephenson (1961, fig. 4B), while the pleopod of the smaller one resembles that figured by Sakai (1939, fig. 19b).

Distribution: New record for eastern Australia. Previously known from Madagascar, Philippines, Carolines, Japan, and Western Australia.

ACKNOWLEDGEMENTS

We are very grateful to Drs J. C. Yaldwyn and D. J. Griffin, of the Australian Museum, or sorting out the interesting material in their collections and sending it, together with the *Endeavour* material, to us. We are also grateful to Mr B. Campbell, of the Queensland Museum, for the loan of *Caphyra unidentata*, and to Mme Tixier-Durivault, of the Muséum National d'Histoire Naturelle, Paris, for the identification of the soft coral *Alcyonium aspiculatum*.

Thanks are also due to the Photographic Section of the University of Queensland for the plates and to the University Research Grants Committee for financial assistance.

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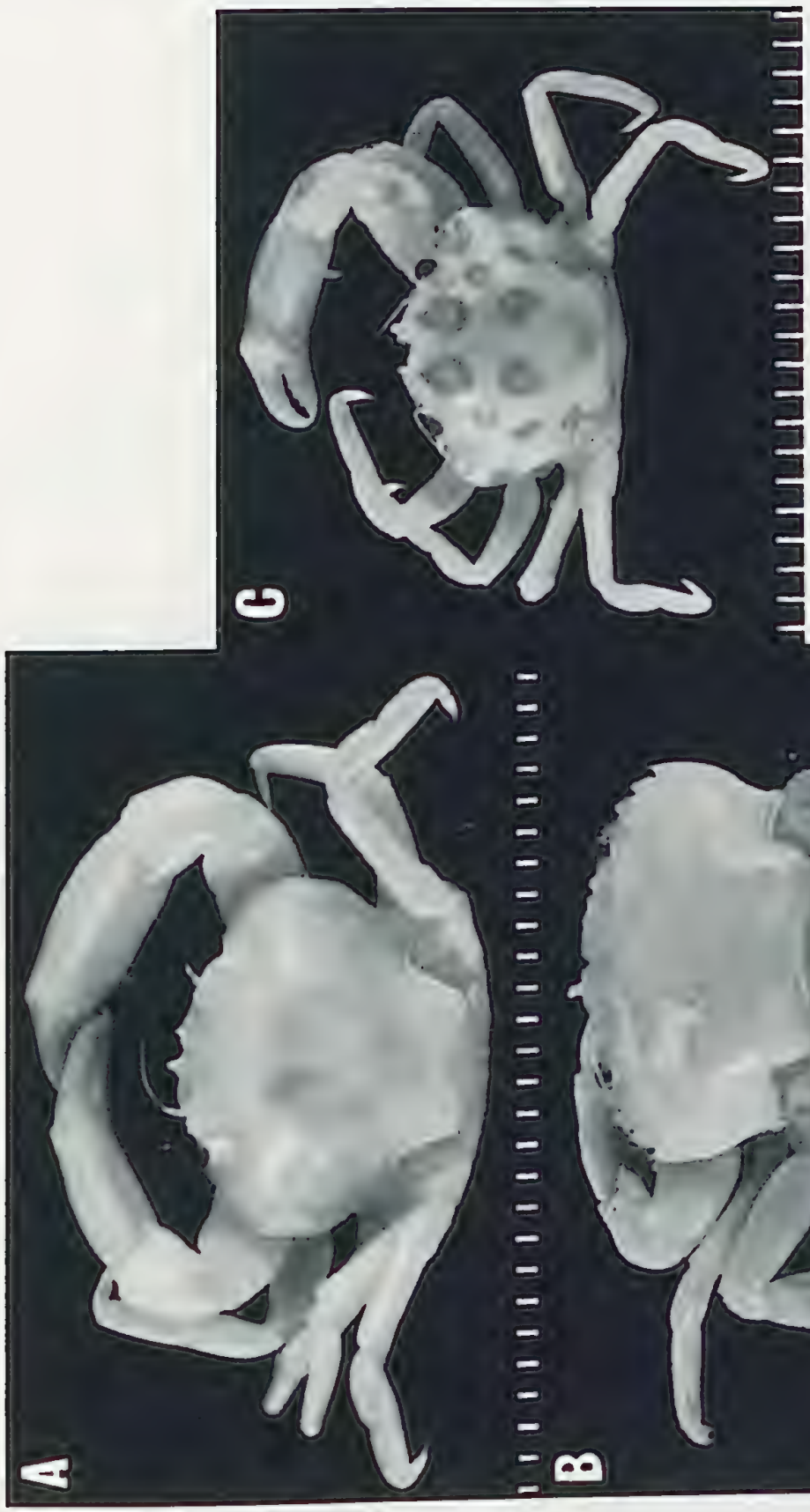

Dorsal views (scale divisions, 1 mm): A, *Caphyra curtipes* n.sp. (holotype); B, *C. holocarinata* n.sp. (holotype); C, *C. yookadai* Sakai.

Robinjohnia tillyardi Martynova, A Mecopteron from the Upper Permian of Belmont, New South Wales

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Plate 44. Fig. 1.

Manuscript received, 29th December, 1967

SUMMARY

Robinjohnia tillyardi Martynova is considered a mecopteron and placed in the Nannochoristidae. The dipteran affinities of the fossil, enumerated by Tillyard in the original reference to this species, have not been recognized.

In 1937 Tillyard described and figured, but did not name, a fossil insect from the Upper Permian of Belmont which he placed in a new order, the Protodiptera, differing from Diptera mainly in possessing four wings. Martynova (1948) named the species *Robinjohnia tillyardi* from the illustrations given in the original publication and subsequently (1961, 1962) referred the species to the suborder Paratrichoptera (order Mecoptera). All four wings and most of the body are preserved. The wings of the left side are outspread, but those of the right side are superimposed on one another and the venation is partly obscured; however, the right side preserves more details of the forewing venation than does the outspread wing of the left side. Tillyard gave a reconstruction of the hindwing which he compared with the forewing

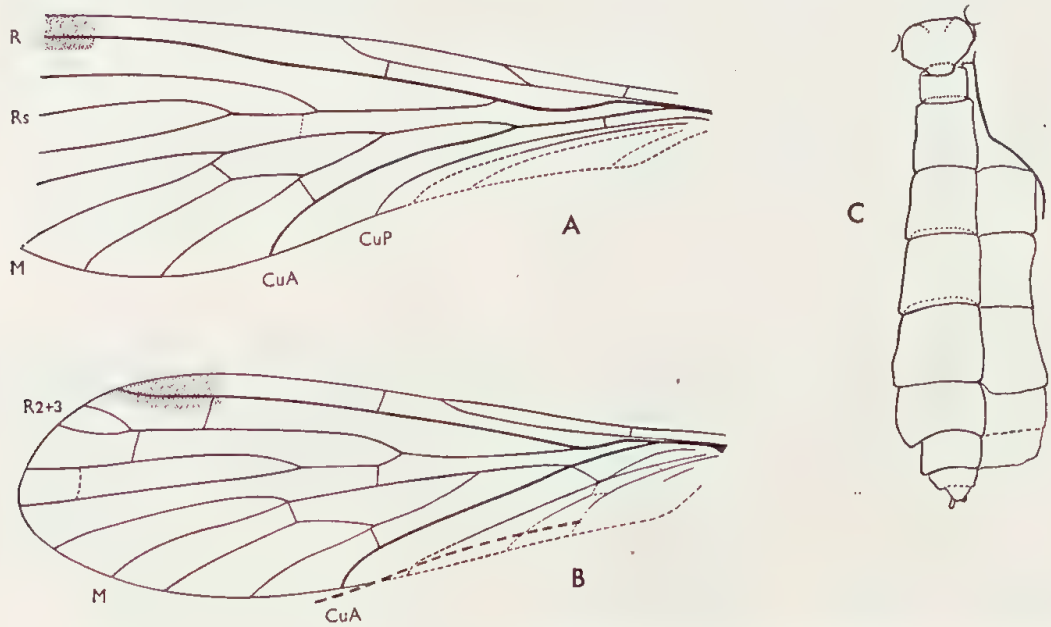

Fig. 1: *Robinjohnia tillyardi* Martynova. X15. A, left forewing. B, left hindwing. C, metanotum and abdomen

of Diptera. The most outstanding characteristics of this reconstruction are not preserved in the fossil. The lighting of the photograph of the fossil had been so arranged that the outline of one of the legs appeared as part of the caudal wing margin and gave a false impression to the wing. As the hindwing is more completely preserved than the forewing it is described first.

Hindwing

Complete except for part of anal field. Length 5 mm. Apex rounded. Sc simple, very short, ending before first forking of Rs. Humeral cross-vein distinct, not more than one-third length of Sc from wing base. R fused with Sc, or very close to it, as far as humeral cross-vein, with a decided bend before origin of Rs and at origin of Rs, simple and straight almost to apex. Pterostigma large but margins indefinite. Rs four-branched; R 2+3 forking close to wing margin. M four-branched, with M 1+2 forking after M 3+4. Discoidal cell distinctly closed by an oblique cross-vein. CuA simple, straight except for distinct downward curvature at wing margin. Basal stem of Cu long, just fusing with 1A before origin of CuA. CuA very oblique, just touching the stem of M. CuP fused to 1A for only a short distance, free portion of CuP well separated from CuA, subparallel to it, straight almost to wing margin. Free portion of 1A short, not fully preserved, first portion nearly traverse and appearing as a cross-vein. 2A short, apex not preserved. 3A preserved only at base.

Forewing

Apex not preserved but in other respects closely similar to hindwing except in anal field. Slightly larger than hindwing. Costal space not expanded. Sc forked, very short, extending very little further than in hindwing. R simple, almost straight except at base. Pterostigma large but not sharply defined. Rs and M similar to hindwing though forking of R 2+3 is preserved in only one wing. (Apex missing, in part, in both forewings). CuA not quite as strongly curved at apex as in hindwing but otherwise similar. CuP subparallel to CuA, strongly curved at wing margin and ending well basad of apex of CuA. CuA and M fused for a considerable distance near their bases. Basal stem of CuA transverse, joining stem of M about level with humeral cross-vein. M separating from CuA just before level of origin of Rs. Anal field crumpled. 1A close to CuP, with apex apparently close to apex of CuP. 2A not clearly preserved.

Body

Head, thorax and abdomen all more or less completely preserved though some structures are not clear. Head preserved in frontal view, small, about as wide as metanotum. Eyes large, somewhat bulging, separated by a distance about equal to their width. Clypeus well developed, lower margin slightly concave. Malar space long. Postocular region rounded, indistinct at meson. Ocelli not defined. Antennae inserted about middle of face, only basal two segments preserved; second segment appears as a pair of raised areas on lower clypeus. Labrum not preserved, but the long malar area suggests that a short rostrum may have been developed. Palps not preserved.

Pronotum and mesonotum badly crushed. Metanotum clearly defined; scutellum small, transverse, with straight anterior and posterior margins; scutum not clearly subdivided. Basal articulation of hindwing clear on one side.

Abdomen complete, shorter than wings. Sternites of anterior segments visible to one side of tergites, apparently due to rupture of the membranes along the left side so that the sternites are displaced to the right and viewed ventrally. Basal tergites preserved in dorsal view. First tergite short; second to sixth subequal, with fifth and sixth decreasing slightly in length; some overlap between tergites visible; seventh both shorter and narrower than sixth. Sternites 1-7 comparable in length with tergites. Apex of abdomen beyond seventh segment very small with no evidence of sternites displaced to one side. Segmentation not clear but apparently with two segments visible. Apex with a distinct cercus on left side and suggestion of one on right. It is suggested that the apical segments of the abdomen are telescoped and that the two visible segments are 9 and 10. Segmentation of cercus not preserved.

Portion of one leg preserved, apparently tibia and base of tarsus.

In general facies the fossil is closely similar to Recent Nannochoristidae. The head is similar but the eyes are less bulging and so the head appears relatively smaller. The specimen is apparently a female as the apex of the abdomen is not swollen and ends in short but distinct cerci. It is similar to that of Recent female *Nannochorista*. This similarity to the Recent species extends to the wing venation. The forewing shows the same marked fusion between the bases of M and CuA and differs mainly in the short Sc and distal branching of R 2+3. There is also close similarity between the hindwings, though small differences occur between the cubital and anal fields, which are not fully preserved in the fossil species. Marked reduction of Sc in both wings is a feature of Recent Bittacidae but other characters of the fossil align it with the Nannochoristidae.

There is no close similarity between the forewing of the fossil and the forewings of Recent Diptera and little purpose is served in comparing the hindwing of the fossil with the forewings of Recent Diptera, for the evolution of the forewing and hindwing in the mecopteroid orders has followed separate paths. In the hindwings of all Recent and fossil Eumecoptera there is some fusion between CuP and 1A. Such fusion does not occur in the forewing. In the forewing of Diptera CuP becomes weak and finally disappears. Diptera differ more fundamentally in venation from Mecoptera in re-alignment of the bases of the main veins.

After original placement in the new family Robinjohniidae (Martynova, 1948) of the suborder Eumecoptera, then in the Permotipulidae (Martynova, 1961, 1962), which was transferred to the suborder Paratrichoptera (for corrected diagnosis of this suborder see Riek, 1956), *Robinjohnia tillyardi* is now placed in the Nannochoristidae of the suborder Eumecoptera, even though there is a small terminal branch on R 2+3 which is absent from all other Recent and fossil species at present referred to the family, for combined with this reduction in venation, there is marked fusion between the bases of M and CuA in the forewing which is so characteristic of this family. Apart from the terminal branching of R 2+3, the short Sc separates *Robinjohnia* from *Nannochoristella* and *Neochoristella*, two genera from the same Upper Permian strata that are also referred to the Nannochoristidae (Riek 1953).

Order **Mecoptera**

Suborder **Eumecoptera**

Family **Nannochoristidae**

Robinjohnia tillyardi Martynova 1948: 42. Holotype F.52312 in the Australian Museum.

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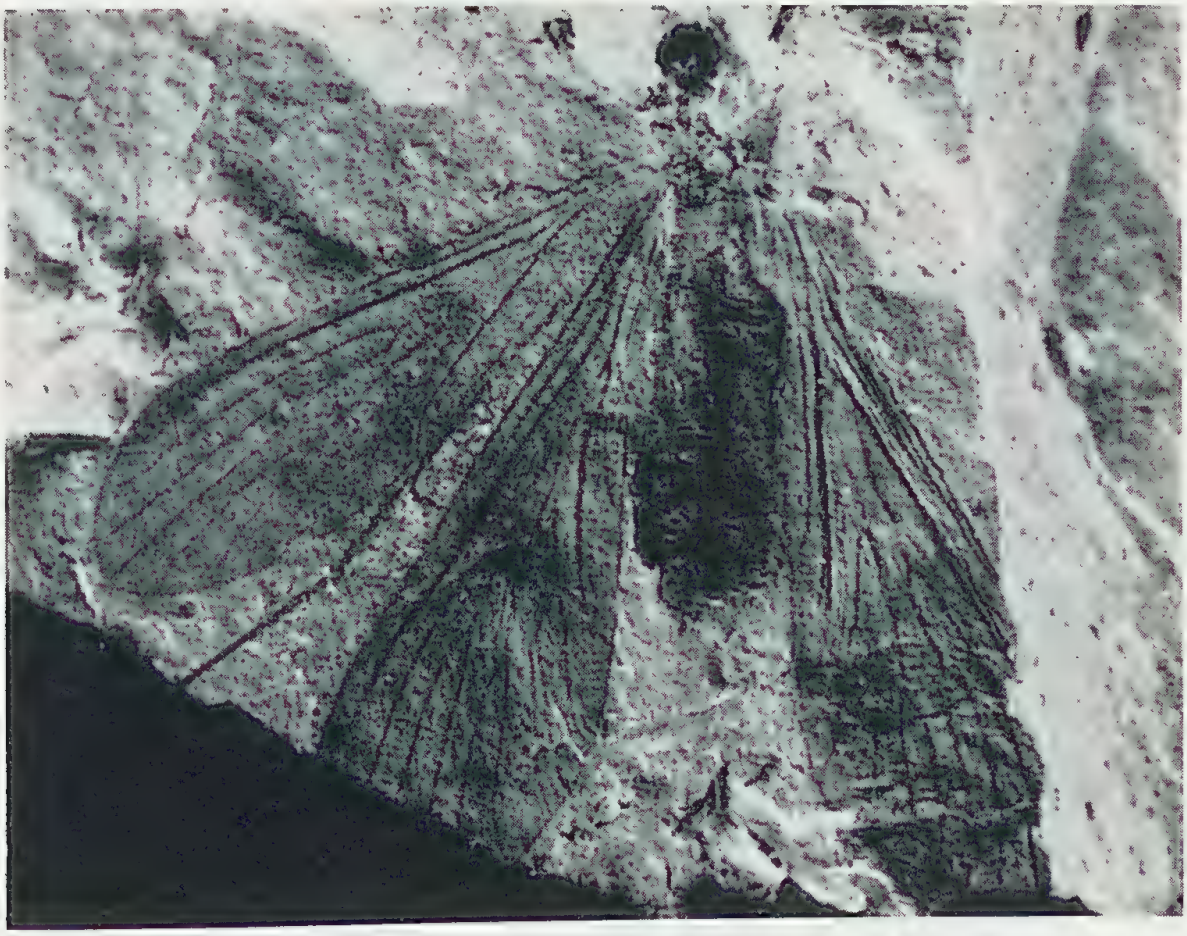

Robinjohnia tillyardi Martynova. X15

UNDESCRIBED FOSSIL INSECTS FROM THE UPPER PERMIAN OF BELMONT, NEW SOUTH WALES

(With an Appendix Listing the Described Species)

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Plate 45. Figures 1–5.

Manuscript received, 29th December, 1967.

SUMMARY

Five unusual or problematic fossil insects from the Upper Permian of Australia are described and illustrated.

The Upper Permian strata at Belmont has yielded a rich and varied insect fauna. Those orders which constitute the dominant elements of the fauna have been studied and the species described in a number of papers by Tillyard (1918, 1919, 1921, 1922, 1924, 1926a, 1926b, 1929, 1935a, 1935b, 1935c), Evans (1943a, 1943b, 1947, 1950, 1956, 1958, 1963), Davis (1942, 1943), Riek (1953), and Kukalova (1966).

Although most of the fossil insect specimens have been studied, there remains unrecorded a small number of unusual and very interesting species. In some cases the affinities of these fossils are obscure while in other cases the remains are rather fragmentary and, although for these reasons one refrains from naming them, they are worthy of discussion even if only to indicate the presence of certain archaic orders of insects which have not previously been recorded from the Australian Permian. As extensive collecting of this horizon is unlikely to be undertaken in the near future, it is considered appropriate that the remaining components of the fauna should be recorded.

Only five specimens are considered worthy of discussion, though there are several interesting fragments that defy classification at present. These are mostly small fragments of relatively large wings. Only one of the five specimens discussed below is formally named.

Specimen F.40701 Australian Museum

(Plate 45, figure 1; Figure 1)

This specimen is considered to be a nymph in which fore and hindwing rudiments and portion of the body are preserved. The impression of the rudiments of the venation preserved on the nymphal wing sheaths indicates relationship to the Plecoptera or Paraplecoptera. Paraplecoptera have not been recorded from this horizon (a fragment described below is referred to the order) but there is a single described species of the Plecoptera. It is suggested that this nymph should be referred to the Plecoptera and considered as being most probably a nymph of *Stenoperlidium permianum* Tillyard, 1935. A comparison between the nymphal venation and that of the adult shows some differences but these are limited to the terminal branches of the veins.

Specimen F.40700 Australian Museum

(Figure 2)

This is the impression of a complete wing very similar to described species of *Permosialis*. This genus has been placed in the Megaloptera but some doubt is expressed here as to its affinities. This wing is well preserved, so the species is named.

Permosialis belmontensis sp. nov.

Length of wing 13.5 mm; width 5.7 mm. Details of the venation are shown in the accompanying illustration.

Type: Holotype, F.40700, in the Australian Museum.

Type locality and horizon: Upper Permian insect beds, Belmont, Australia.

Specimen F.40038 Australian Museum

(Figure 3)

This specimen is not well preserved but there seems little doubt that it is a representative of the Megasecoptera, suborder Eumegasecoptera.

Specimen F.43142 Australian Museum and counterpart F.43141

(Plate 45, figure 2; Figure 4)

These two impressions preserve the extreme apical portion of a very large wing that can be compared with species of Liadotypidae (order Meganisoptera).

Specimen F.41067 Australian Museum

(Figure 5)

This fragment could be referred to the Paraplecoptera and compared with representatives of the Lemmatophoridae, but the very fragmentary nature of the wing makes any placement doubtful. It represents portion of a relatively large wing, with a less distinct underlying wing (? hindwing) and with the apical portion of each wing folded back on itself.

THE DESCRIBED AUSTRALIAN FOSSIL INSECTS FROM THE UPPER PERMIAN OF BELMONT

Odonata	*Polytaxineura stanleyi* Till., 1935b: 376
Plecoptera	*Stenoperlidium permianum* Till., 1935c: 387
	[*Antitaxineura anomala* Till., 1935b: 383]
Glosselytrodea	*Permoberothella perplexa* Riek, 1953: 80
Psocoptera	*Austrocypha abrupta* Till., 1935a: 278
	A. baretti Till., 1935a: 278
	Austropsocidium pincombei Till., 1935a: 268
	A. stigmaticum Till., 1935a: 268
	Lophiocypha permiana Till., 1935a: 275
	L. stanleyi Till., 1935a: 276
	L. thysanella Till., 1935a: 276

L. maxima Davis, 1942: 121
Lophioneura ustulata Till., 1921: 420
L. angusta Till., 1935a: 278
L. (?) *conjuncta* Till., 1926a: 29
Megapsocidium australe Till., 1935a: 269
Stenopsocidium elongatum Till., 1935a: 270.
Zoropsocus delicatulus Till., 1935a: 273
Z. stanyleyi Davis, 1942: 119
Zygopsocus permianus Till., 1935a: 271

Hemiptera

Actinoscytina belmontensis Till., 1926a: 18
Anomaloscytina metapteryx Davis, 1942: 113
A. incompleta Evans, 1943a: 189
Austroprosbole maculata Evans, 1943a: 182
Austroscytina imperfecta Evans, 1943a: 180
Beaconiella fennahi Evans, 1963: 21
B. multivenata Evans, 1963: 22
Bekkerscytina primitiva Evans, 1958: 112
Belmontocarta perfecta Evans, 1958: 113
Belpsylla reticulata Evans, 1943: 193
Clavopsyllidium minutum Davis, 1942: 117
Elliptoscarta ovalis Till., 1926a: 17
Eochiliocycla angusta Davis, 1942: 114
Eopsyllidium delicatulum Davis, 1942: 115
Eoscytina migdisovae Evans, 1958: 110
E. incompleta Evans, 1958: 111
Eupincombea postica Davis, 1942: 114
Homaloscytina plana Till., 1926a: 16
Mitchelloneura permiana Till., 1921: 416
Orthoscytina mitchelli Till., 1926a: 10
O. quinquemedia Till., 1926a: 11
O. indistincta Till., 1926a: 11
O. subcostalis Till., 1926a: 11
O. irregularis Till., 1926a: 12
O. belmontensis Till., 1926a: 13
O. obliqua Till., 1926a: 13
O. pincombei Till., 1926a: 14
O. tetraneura Till., 1926a: 15
Palaeovicia incerta Evans, 1943a: 189
Paraknightia magnifica Evans, 1943a: 180
Permagra distincta Evans, 1943b: 7
Permobrachus magnus Evans, 1943a: 183
P. dubia (Till.), 1926a: 24
Permocentrus trivenulata (Till.), 1926a: 20
Permodiphthera robusta Till., 1926a: 24
Permoglyphis belmontensis Till., 1926a: 22

Permojassus australis Till., 1926a: 8
P. dubius Till., 1926a: 8
Permopsyllidium mitchelli Till., 1926a: 28
P. affine Till., 1926a: 28
Permopsyllidops stanleyi Davis, 1942: 117
Permopsylloides insolita Evans, 1943a: 193
Permoscarta mitchelli Till., 1918a: 728
Permothea latipennis Till., 1926a: 28
Permotheëlla scytinopteroides Davis, 1942: 116
Permovicia obscura Evans, 1943a: 189
Pincombea mirabilis Till., 1922: 282
Protopincombea obscura Evans, 1943a: 193
Protopsyllidium australe Till., 1926a: 26
P. sinatum Davis, 1942: 117
Protopsyllops minuta Evans, 1943a: 192
Psocopsyllidium media Davis, 1942: 116
Psocoscytina bifida Davis, 1942: 112
Psyllidella magna Evans, 1943a: 192
Psyllidiana davisia Evans, 1943a: 192
Stanleyana pulchra Evans, 1943a: 188
Stenoglyphis kimblensis Evans, 1947: 43
Stenoscytina australiensis Till., 1926a: 16
Stenovicia angustata Evans, 1943a: 189
Triassodoecus chinai Evans, 1963: 23
Tripsyllidium wadei Evans, 1956: 238
Tychticoloides belmontensis Evans, 1963: 21

Mecoptera

Agetochoristella adscita Riek, 1953: 68
[*Aphryganoneura anomala* Till., 1926: 276]
Belmontia mitchelli Till., 1919: 234
syn. *Parabelmontia permiana* Till., 1922: 286
Mesochorista australica (Till.), 1918: 733
syn. *Permochorista mitchelli* Till., 1918: 734
P. sinuata Till., 1922: 287
P. affinis Till., 1922: 288
P. collinsi Till., 1926b: 269
P. pincombei Till., 1926b: 269
P. angustipennis Till., 1926b: 270
P. osbornei Till., 1926b: 271
P. inaequalis Till., 1926b: 272
M. jucunda (Till.), 1926b: 268
M. dubia Riek, 1953: 63
M. phipa Riek, 1953: 63
Mesopanorpodes belmontensis Riek, 1953: 70
M. robustus Riek, 1953: 71
Nannochoristella reducta Riek, 1953: 74

	Neoageta elongata Riek, 1953: 67
	Neochoristella optata Riek, 1953: 74
	Neopetromantis australis Riek, 1953: 67
	Parachorista pincombeae Till., 1926b: 273
	syn. *P. warnerensis* Till., 1926b: 273
	P. splendida Till., 1926b: 274
	P. (?) *bairdae* Till., 1922: 284
	Permomerope australis Till., 1926b: 275
	P. nanus Riek, 1953: 57
	Permotipula patricia Till., 1929: 779
	Phipoides elegans Riek, 1953: 66
	Prochoristella megaloprepia Riek, 1953: 71
	P. anagaura Riek, 1953: 72
	P. exilis Riek, 1953: 72
	P. pusilla Riek, 1953: 73
	P. belli (Till.), 1926: 272
	P. concinna Riek, 1953: 73
	Robinjohnia tillyardi Martynova, 1948: 42
	Xenochorista splendida Riek, 1953: 69
	X. sobrina Riek, 1953: 69
Neuroptera	*Archeosmylus pectinatus* Riek, 1953: 86
	Permithone belmontensis Till., 1922: 290
	syn. *Permosmylus pincombeae* Till., 1926b: 281
	P. oliarcoides Till., 1926b: 278
	P. neoxenus Riek, 1953: 82
	Permopsychops belmontensis Till., 1926b: 281
	syn. *Permithone venosa* Davis, 1943: 11
	Permorapisma biserialis Till., 1926b: 279
	syn. *P. triserialis* Till., 1926b: 279
Trichoptera	*Cladochorista belmontensis* Till., 1926b: 273
Diptera	*Permotanyderus ableptus* Riek, 1953: 75
	Choristotanyderus nanus Riek, 1953: 76
Coleoptera	*Permosyne belmontensis* Till., 1924: 433
	P. affinis Till., 1924: 433
	P. mitchelli Till., 1924: 433
	P. pincombeae Till., 1924: 433
Protelytroptera	*Austrelytron tillyardi* Kukalova, 1966: 98
	Chanoselytron gingiva Kukalova, 1966: 109
	Dermelytron conservativum Kukalova, 1966: 106
	D. pigmentatum Kukalova, 1966: 108
	Elytrathrix hirsuta Kukalova, 1966: 102
	Permofulgor belmontensis Till., 1918a: 731
	(syn. *P. indistinctus* Till., 1922: 280)*
	Permophilus pincombei Till., 1924: 430

* The holotype of *Permofulgor indistinctus* is a counterpart of the holotype of *Permofulgor belmontensis*.

P. (?) *minor* Till., 1924: 431
P. hirtus Kukalova, 1966: 100
P. capulus Kukalova, 1966: 100
Phyllelytron folium Kukalova, 1966: 94
P. petalon Kukalova, 1966: 95
P. granulatum Kukalova, 1966: 95
P. melinum Kukalova, 1966: 95
Protocoleus mitchelli Till., 1924: 434
Psychelytron progressivum Kukalova, 1966: 108
Stenelytron enervatum Kukalova, 1966: 104
Xenelytron ligula Kukalova, 1966: 105

incertae sedis

Antitaxineura anomala Till., 1935b: 383
Aphryganoneura anomala Till., 1926b: 276
Permocephalus knighti Evans, 1943b: 8
Permocapitus globulus Evans, 1943a: 194

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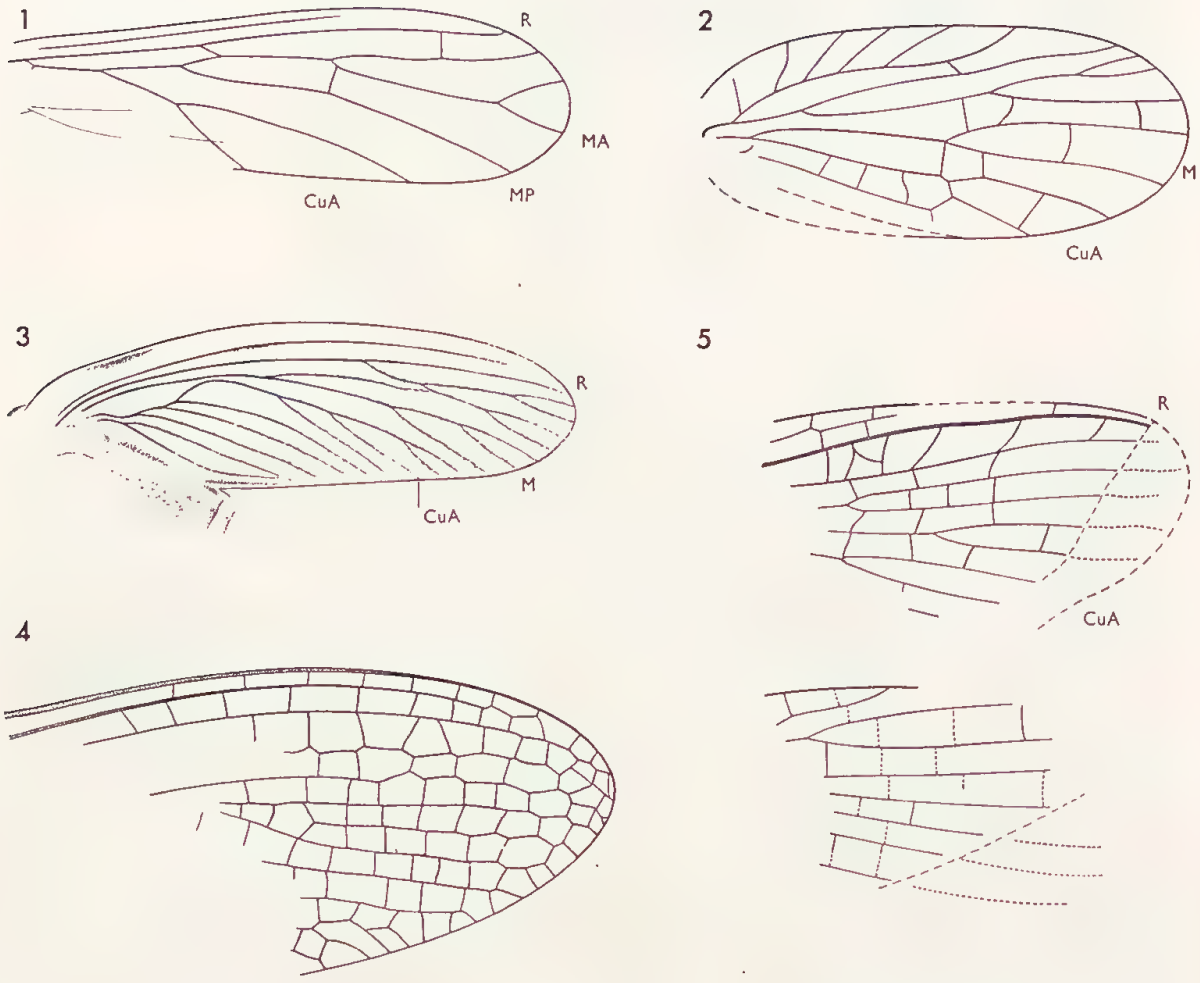

Figure 1: Forewing of nymphal insect, very probably of *Stenoperlidium permianum* Tillyard 1935. X5.
Figure 2: Forewing of *Permosialis belmontensis* sp. nov. X4.
Figure 3: Australian Museum F.40038. Order Megasecoptera, suborder Eumegasecoptera. X11.
Figure 4: Australian Museum F.43142 and F.43141. Order Meganisoptera. X4.
Figure 5: Australian Museum F.41067. Order Paraplecoptera. Separated wings. X4.

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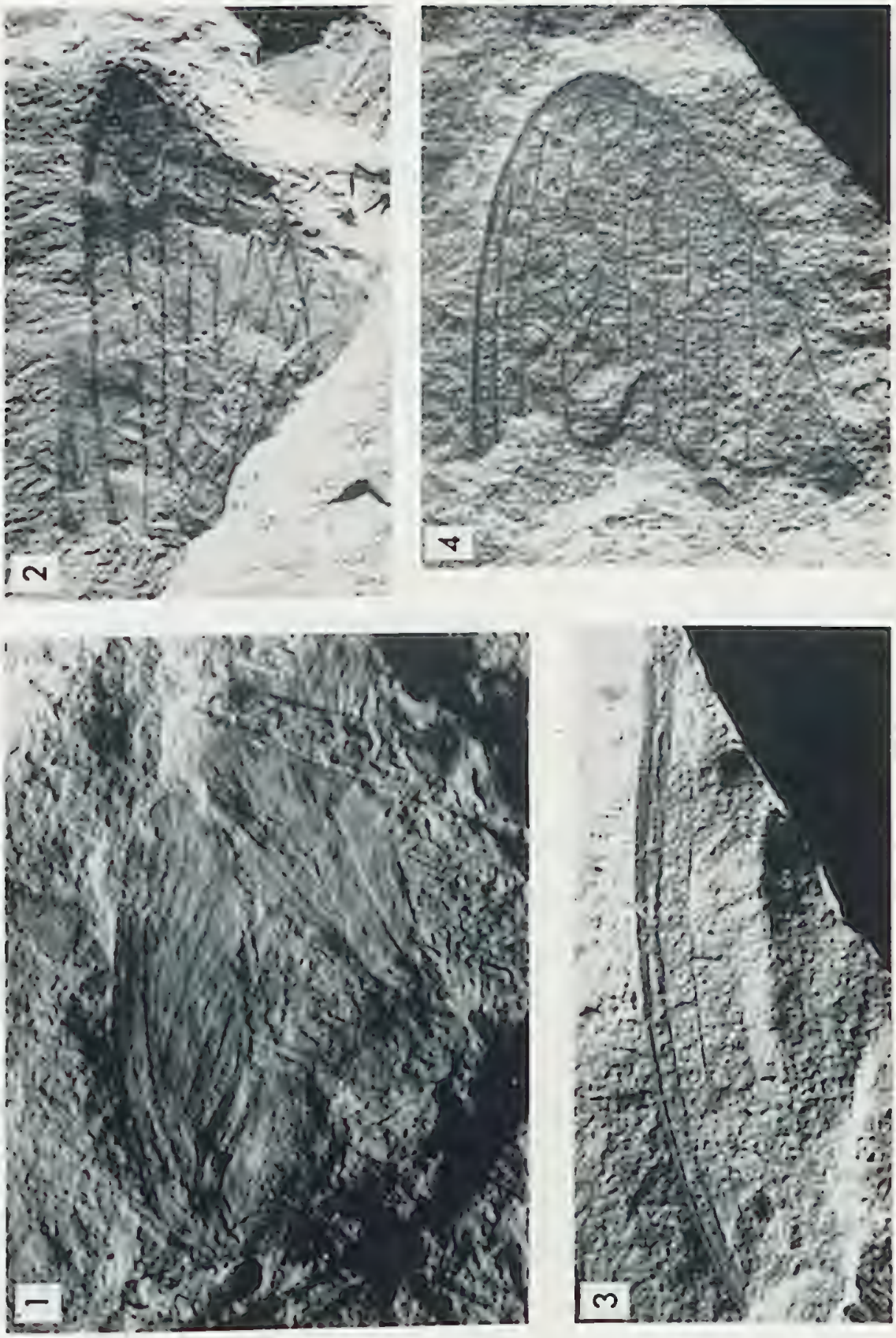

Figure 1: Australian Museum F.40701; nymphal insect, showing fore and hind wing-pads, very probably nymph of *Stenoperlidium permianum* Tillyard 1935; X5. Figure 2: Australian Museum F.41067; apical wing fragments; order Paraplecoptera; X6. Figure 3: Australian Museum F.43141; apex of wing; order Meganisoptera; X6. Figure 4: Australian Museum F.43142; counterpart of figure 3: X6

ON THE OCCURRENCE OF FOSSIL INSECTS IN THE MESOZOIC ROCKS OF WESTERN AUSTRALIA

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Plate 46.

Manuscript received, 29th December, 1967.

SUMMARY

A new insect-bearing horizon is placed on record. A beetle elytron, the pronotum of possibly the same species of beetle, and a cockroach forewing are described. The probable age of the sediments is discussed.

A small collection of insect fossils has been made in the Hill River area of Western Australia. As additional diagnostic material has not become available, the occurrence of this new insect-bearing horizon is placed on record. The only well preserved insect remains are beetle elytra. Impressions of other insects are fragmentary and not clearly defined.

Fossil insects have been obtained from the following localities:

Hill River, 1 mile sheet.

Grid reference 192521. Four beetle elytra and pronotum of a beetle.

191523. One beetle elytron and pronotum of a beetle. Forewing of a cockroach.

241550. One beetle elytron.

The cockroach forewing, F.52316, is too poorly preserved for specific description but it does show some diagnostic features. Sc was very short and apparently unbranched. The stem of R is almost straight after the initial basal curvature, and the branches of R are mostly simple. Such a combination of characters would place the species in the Mesoblattinidae and possibly in the genus *Austroblatulla*, described from the Triassic of Denmark Hill, Queensland. The Mesoblattinidae have a range from late Paleozoic to Jurassic.

As cockroaches are not known to occur in the Australian Permian, although other insect remains are common, a Triassic age seems most probable for the stratum on the basis of this one fossil.

Beetles occur first in Australia in the Upper Permian of Belmont, New South Wales, but are not common until the Triassic. As elytra are not one of the most diagnostic characters used in the classification of beetles, the classification of fossil elytra is rather arbitrary. One well preserved elytron from locality 191523 is compared with that of a species, placed in the genus *Mesothoris*, from the Triassic of Denmark Hill, Queensland. A well preserved pronotum is considered to be another part of the same fossil species.

This beetle elytron supports a probable Triassic age for the sediments but more diagnostic fossils are necessary for confirmation of this age determination.

Order	Coleoptera
Family?	Tenebrionidae
Genus	*Mesothoris* Tillyard.

The genus was erected for a Triassic elytron from the Denmark Hill beds. Tillyard (1916: 23) placed the genus in the Cerambycidae and compared it with the Recent *Thoris*. He also compared it *with Omma* (Cupedidae). Dunstan (1923: 58), after an examination of additional material which he referred to the genus, considered that it had no affinity with *Thoris* (nor with *Omma*).

Comparison with other Recent beetles shows that there is a greater similarity between these Triassic fossils and the family Tenebrionidae. This correlation is strengthened by evidence derived from this Western Australian species.

Mesothoris westraliensis sp. nov.

Holotype: elytron F.52315, in the Australian Museum, Sydney.
Locality and horizon: Hill River, 1 mile sheet, grid reference 191523, probable Triassic strata.

Elytron. Length 7 mm, greatest width 2.3 mm, width at base 1.7 mm; apex not fully preserved; surface entirely sculptured, sculpture formed by the intersection of nine or ten broad, flat longitudinal ridges with similarly spaced traverse ridges, forming an areolate pattern, the areolae rather square and about one and a half times as wide as the flattened ridges. The transverse ridges are somewhat stepped across the elytron. Inflexed margin of elytron flattened in preservation and clearly visible to apex, finely ornamented, with a distinct submarginal groove over the basal half, its basal angle acute, 0.4 mm wide towards base. The slight widening of the elytron in the middle is probably due to a flattening of this more convex portion. The humeral angle is distinct but not very strongly developed, and the anal notch is very small. Although not fully preserved, the apex is rather acute.

The tentative placement of this fossil in the Tenebrionidae is supported by the presence of a coleopteran pronotum F.52313 in strata from a closely adjoining locality. This pronotum is 3.8 mm across at its caudal margin. Such a size corresponds very well with an elytron 1.7 mm wide at its base. As the other beetle elytra from this deposit are very much smaller it is not unreasonable to assume specific association of these two fossils. The pronotum is strongly convex from side to side and slightly so from anterior to posterior border. Close to the lateral margins there is some evidence of compression wrinkling which, at first sight, gives the impression of ornamentation. The pronotum is otherwise smooth. The lateral margins are strongly convex and the caudal margin is transverse. The postero-lateral angles are acutely produced.

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Figures 1–2: *Mesothoris westraliensis* sp. nov. Holotype elytron. F.52315. 1, X10. 2, X7. Reversed lighting

Figure 3: ? *Mesothoris westraliensis*. F.52313. Pronotum X7.

Figure 4: Beetle elytron. indet. F.52314. X7.

Figure 5: Beetle elytron. indet. F.52317. X7.

RE-EXAMINATION OF TWO ARTHROPOD SPECIES FROM THE TRIASSIC OF BROOKVALE, NEW SOUTH WALES

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Figures 1 - 3

Manuscript received 29th December, 1967

SUMMARY

The two fossil arthropod species, *Austrolimulus fletcheri* Riek and *Synaustrus brookvalensis* Riek, are re-examined and reconstructions based on their apparent structure are presented for comparison with related species. A modified reconstruction of *Euthycarcinus kessleri* Handlirsch is also included for comparison with *Synaustrus*.

The Triassic sediments at Brookvale have yielded a small but most interesting fossil assemblage consisting mainly of fish, insect and plant remains but including a "unio", a stegocephalian head, a syncarid, Conchostraca (Wade, 1935) and the two arthropod species reviewed in this paper, a xiphosuran and a branchiopod.

The fossil assemblage is in accord with a freshwater origin of these sediments and the xiphosuran was most probably an inhabitant of freshwaters rather than a transient from marine or brackish waters. The well preserved nature of all the fossils and their completeness, combined with the relatively large size of the insect wings, would seem to indicate undisturbed water conditions at least at the time the fossils were embedded and very probably indicates drying-out of the water body. The suggestion that the body of water was drying out is supported by the manner of preservation of one of the specimens of *Synaustrus brookvalensis* Riek. In this individual arthropod the thin lateral body wall is wrinkled and deflected back, as though the animal had crawled through drying mud before it succumbed.

The insect fossils are mostly complete, well preserved wings, in some of which the pigmentation pattern is still evident. This is not usual in fossil wings, though it is known to occur in other deposits. It is very probably a reflection of some unusually favourable conditions of preservation which resulted also in the preservation of the uncalcified cuticle that occurs in xiphosurans, Conchostraca and other Branchiopoda. The insects have been described in a number of papers by Tillyard (1925), McKeown (1937), Riek (1950, 1954) and Evans (1956, 1963).

The two arthropods reviewed in this paper were described by Riek (1955, 1964). The xiphosuran is known from a single complete specimen. There are three specimens of the unusual branchiopod and, although one of these is complete, some details of its external morphology remain unknown, for this is the specimen referred to above in which there has been considerable distortion prior to preservation.

G 64310–1

Class **MEROSTOMATA**
Subclass **Xiphosura**
Superfamily **Limulacea**
Family **Austrolimulidae** Riek, 1955
Austrolimulus fletcheri Riek, 1955: 281

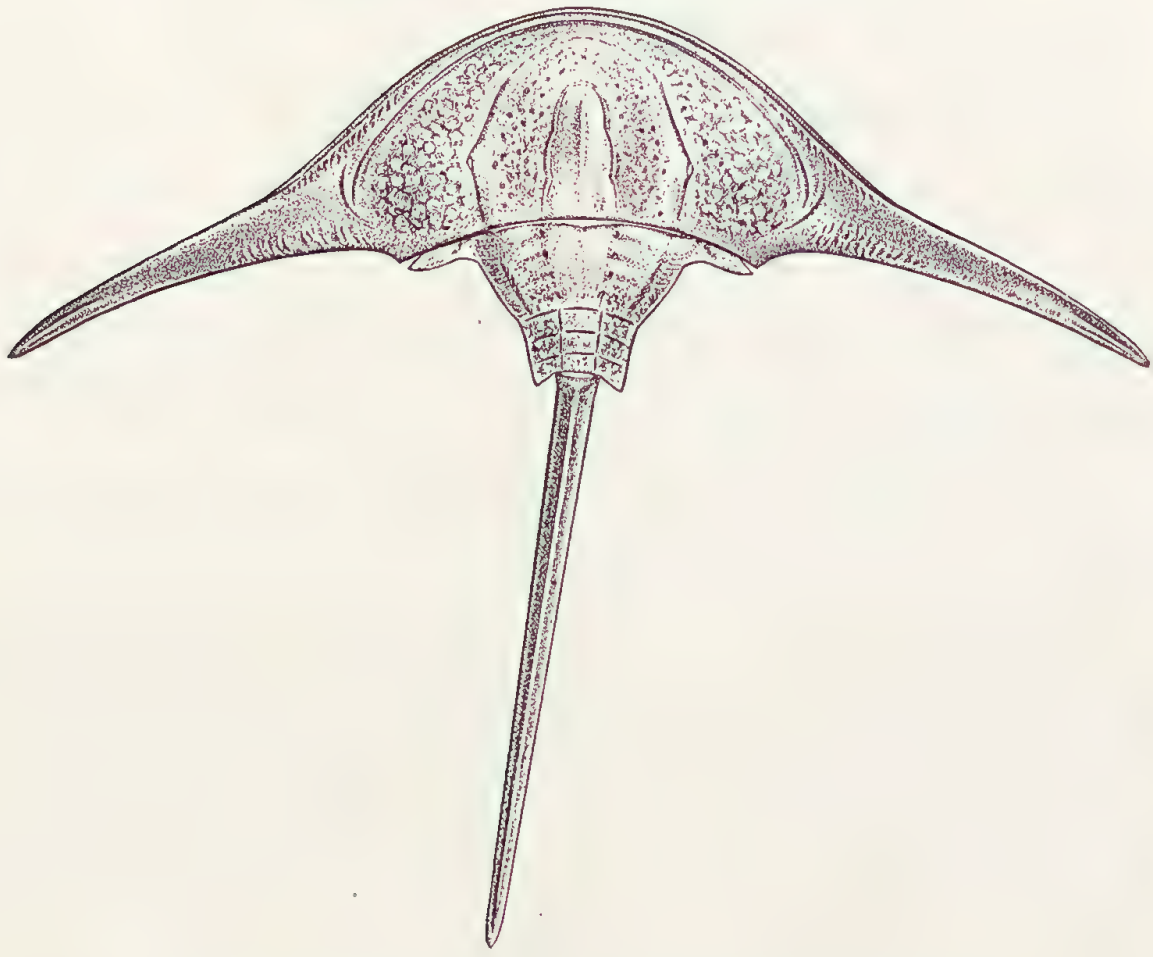

Figure 1 : Reconstruction of *Austrolimulus fletcheri* Riek, dorsal view.

The family Austrolimulidae occupies a position intermediate between the Paleolimulidae (Raymond, 1944) and the Mesolimulidae (Størmer, 1952). In the Paleolimulidae the posterior segment of the opisthosoma is clearly defined and is stated to be movable (Størmer, 1955). In the Mesolimulidae all the segments of the opisthosoma are consolidated and segmentation is not clearly preserved. In the Austrolimulidae the posterior two segments of the opisthosoma are clearly defined, though ankylosed. The segment in front of these is also apparently defined, though less distinctly so, for there is a very distinct change in direction of the lateral margin of the opisthosoma at this point and a difference in the manner of preservation between the posterior three segments and the remainder of the body with the posterior three segments represented by ventral views and moulds, whereas the anterior portion is preserved as external and internal moulds of the dorsal surface. There is no evidence of lobing of the lateral margins of the opisthosoma, and if spines were present they were very small. The anterior free lobe of the opisthosoma is well developed. As the pleural region of the opisthosoma is very reduced, the posterior margin of the free lobe joins the lateral margin of the opisthosoma without a re-entrant angle.

Possibly the most distinctive feature of *Austrolimulus fletcheri* is due to the development of the genal spines which arise entirely anteriorly of the caudal margin of the prosoma, and even their apices extend only slightly behind this line. *Austrolimulus* shows most similarity to *Psammolimulus*, particularly in the structure of the opisthosoma and to a less extent in the genal spines.

Austrolimulus fletcheri was figured in the original description and a reconstruction based on photographs was presented by Novojilov (1962: 399). A reconstruction (figure 1) based on the original material is reproduced in this review. The suture between the anterior portion of the opisthosoma and the third segment from its caudal end is indicated, though this is partly inferred rather than observed. The ophthalmic ridge is defined laterally but the eye is inferred to some extent through the change in direction of the ridge at this point. The caudal style may be proportionally longer than indicated, but it is certainly not shorter.

Class **CRUSTACEA**

Section **Branchiopoda**

Subclass **Euthycarcinoidea** Gall and Grauvogel, 1964

Family **Euthycarcinidae** Handlirsch, 1914

Synaustrus brookvalensis Riek, 1964: 328

The excellent review of *Euthycarcinus kessleri* Handlirsch, 1914, from the Vosges region of France, by Gall and Grauvogel (1964), has enabled clarification of many puzzling features of *Synaustrus brookvalensis* Riek, 1964, from Brookvale, Australia, and has indicated that there is a very close relationship between these two Triassic fossil species. The similarity is such that in all probability some of the described differences may even be due to errors in interpretation of the fossil remains rather than that they represent valid differences. The most striking differences are concerned with the structure of the antennae and other features of the head, but most of these differences are possibly subject to sexual dimorphism. There is also a difference of interpretation of the last thoracic or first abdominal sternite.

In dorsal view there is great similarity in body form. The interpretation of a distinct glabellar region in *Synaustrus* was in error, and this presumed structure reflects the extent of the very large labrum seen through the flattened dorsal surface. In *Synaustrus* there is no evidence of overlap between the tergal plates of the thoracic shield, whereas there is apparently a distinct overlap in *Euthycarcinus* (see Gall and Grauvogel, plate 1 and plate 3, figure 1).

In ventral view the main difference in body form lies in the development of the twelfth post-cephalic sternite. In *Euthycarcinus* (plate 4) this is regarded as a (separate) first abdominal sternite and the abdomen is considered to possess five sternites but only four tergites. It is suggested that this is not a complete sternite but represents the development of a brood-pouch from the last thoracic sternite of a female specimen (as in Recent Anostraca, though there it is regarded as the first abdominal segment). There would then be only four sternites as well as four tergites in the abdomen. Gall and Grauvogel show eleven serially arranged pairs of appendages; these appendages arise from the junction between segments so that the twelfth segment can be considered to have lost its appendages, though Gall and

Grauvogel consider that it is the first segment that is without appendages. The insertions of the appendages are very clear in *Synaustrus*. They arise from the middle of each segment and it was considered originally that twelve pairs were present, but some doubt was expressed about the presence of appendages on the twelfth segment.

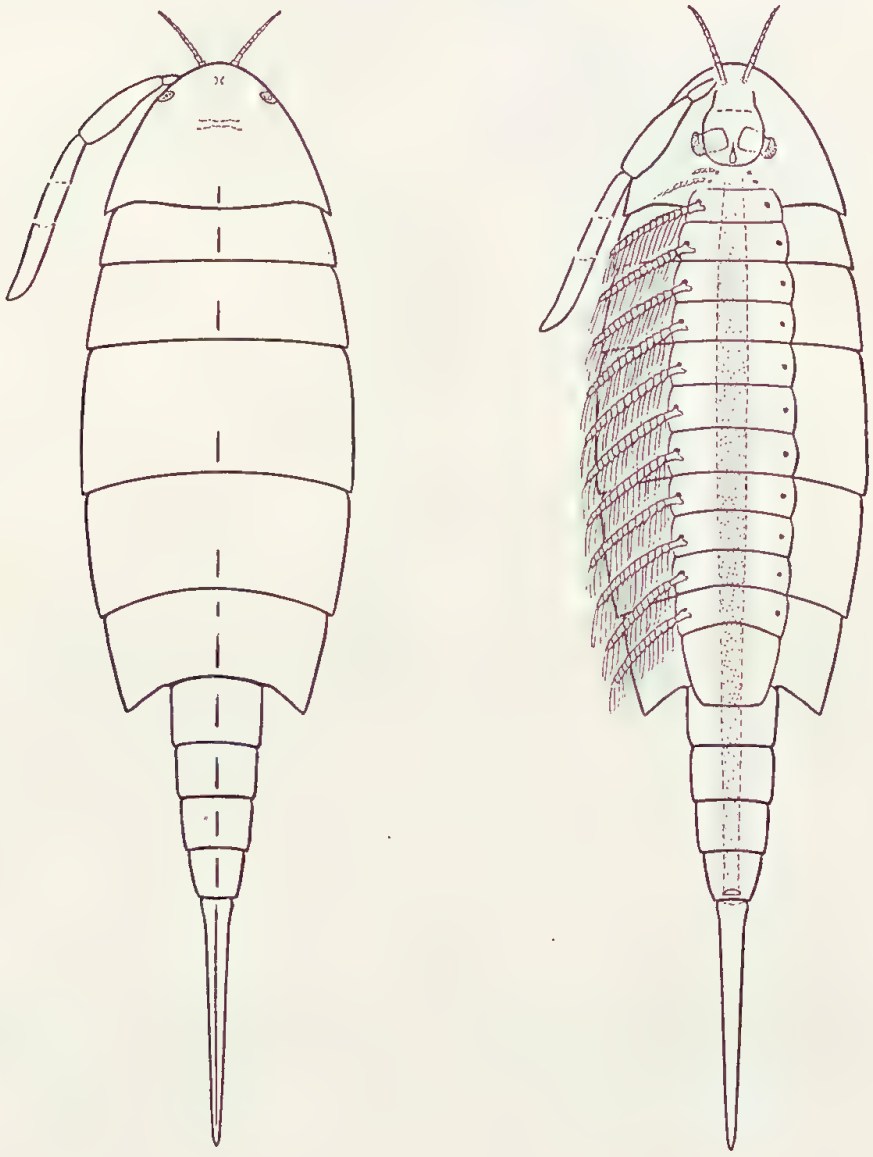

Figure 2 : Reconstruction of *Syanustrus brookvalensis* Riek, dorsal and ventral views.

In *Synaustrus* some doubt was also expressed as to whether the first of these appendage-bearing segments represented a free first thoracic segment or was incorporated in the head tagma, as was considered to be the case in *Euthycarcinus*. It is suggested that all these eleven appendage-bearing segments are thoracic and that the thorax consists of twelve segments. There is then great similarity between these fossils and Recent Anostraca in this respect, though in the Anostraca the twelfth segment is regarded as the first abdominal segment.

There is apparently great similarity in the structure of all the post-cephalic appendages. These are regarded as simple multisegmented processes with an enlarged basal segment. There are long mariginal hairs, apparently one per segment, in *Euthycarcinus*, but these are not evident in *Synaustrus*. The shape of the individual segments is rather more clearly defined in *Euthycarcinus* than in *Synaustrus* but in the latter genus the insertions of the appendages and the enlarged basal segment with the development of a weak gnathobase are distinct (Riek, plate 35, figure 3). The long marginal fringe would indicate that these appendages were used for swimming.

There are marked differences in fact as well as in interpretation in the structure of the appendages of the head tagma of *Synaustrus* and *Euthycarcinus*. The appendages of the head in *Euthycarcinus* are interpreted by Gall and Grauvogel as first and second antennae, mandibles and buccal complex. The buccal complex was considered to consist of two pairs of maxillae. A structure comparable to a hypopharynx was also recognized. Some doubt was expressed as to the presence of a second pair of antennae. If the mouthparts were as highly evolved as Gall and Grauvogel suggest, one would expect the mandibles to be more closely associated with the maxillae and, possibly the maxillae to be less widely spaced from the following appendages.

An alternate explanation is proposed in this review for the structures interpreted as mandibles and buccal complex. These are only well preserved in the specimen that Gall and Grauvogel regard as an exuvium (with which I would concur). It is suggested that the former are a pair of median ocelli and that the latter represent an irregularly folded median zone of the dorsal cuticle comparable to that which occurs in Recent Notostraca and, in reduced form, in Anostraca. No other head structures are indicated on this fossil which would tend to support the view that only structures of the dorsal surface are preserved. The eyes are not evident in this particular fossil but this is the usual condition in an exuvium. In other specimens that are not regarded as exuviae the above structures are indistinct but the eyes are very prominent. Another three pairs of structures are also indicated with the anterior two pairs almost if not quite as prominent as the eyes. These were interpreted as muscle impressions by Gall and Grauvogel. They are considered in this review to represent the insertions of appendages and the muscles associated with their insertions. The posterior, less distinct pair correspond in position with the first of the serially arranged thoracic appendages but are somewhat closer together than the insertions of the following appendages. The anterior two pairs are less easily interpreted. The insertions of the posterior of these two pairs are stronger (and more widely separated) than the anterior pair. This development could be correlated with the presence of two pairs of antennae of which the second pair is enlarged; however, it seems more probable that they represent the insertions of a single pair of antennae and a pair of mandibles or mandible-like structures, for Gall and Grauvogel show on plate 3, figure 3 a specimen in which the digestive tract extends almost to the middle of the head tagma to the level at which this pair of

strong, widely-spaced dark areas is seen in other specimens. The small structure interpreted by Gall and Grauvogel as the second antenna may represent the appendage of a post-mandibular segment (maxilla) and this could account for its reduction in size.

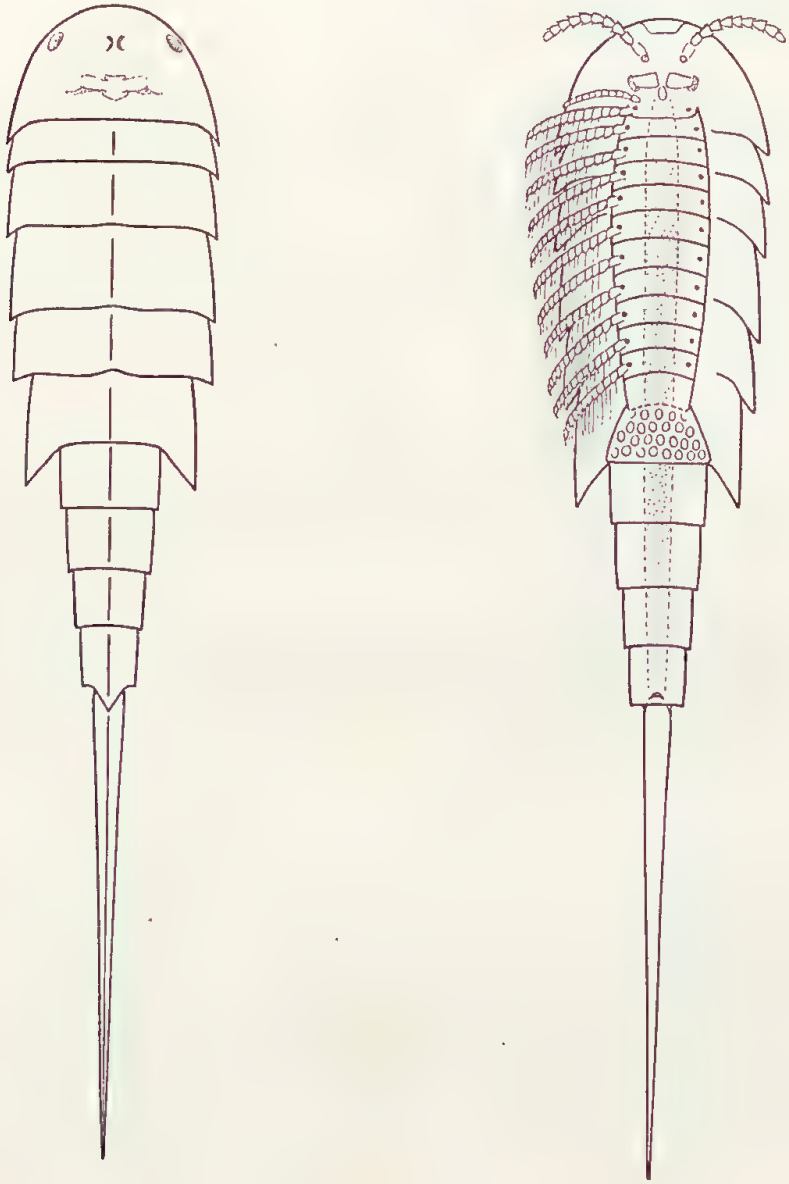

Figure 3 : Reconstruction of *Euthycarcinus kessleri* Handlirsch, dorsal and ventral views, modified from Gall and Grauvogel, 1964.

The head tagma of *Euthycarcinus* is thus interpreted in this review of its structure as consisting of a dorsal shield bearing a pair of ocelli placed close together towards the anterior margin, a pair of sessile laterally placed eyes situated in the anterior half and with an irregular transverse groove about the middle of its length, impressed mainly at meson. There is a doublure of the anterior margin to produce a small labrum. Ventrally the head tagma bears at least three pairs of appendages, anteriorly a pair of antennae inserted close to the lateral margins of the labrum, a large mandible or mandible-like structure and posteriorly a pair of appendages similar to the serially arranged thoracic appendages but inserted closer together than on the following segments. There was also quite probably another post-mandibular segment in which the appendages were reduced or virtually absent and a pair of very small first antenna. If this interpretation is correct then there is great similarity between *Euthycarcinus* and Recent Anostraca.

Re-examination of the head of *Synaustrus* shows the development of a very large labrum extending more than half way to the caudal margin and free of the ventral surface of the head over its distal two-thirds. This structure was originally interpreted as a glabella and its subdivisions as possibly representing segmentation ventrally of the head tagma. The basal segment of each first antenna is distinct at the anterior margin of the head. These were originally interpreted as the lateral margins of a small labrum. There has been no further clarification of the structure of the second antenna, though it is possibly only three-segmented with a small basal segment, a large, expanded second segment and a long parallel-sided apical segment from comparison with the enlarged second antenna in male Anostraca. The mandibles are not distinct, though the outer margin of their insertions may be visible lateral to the labrum. No structures between the possible mandibles and the first thoracic appendages are preserved but if the relationship to Anostraca is valid then there were two pairs of reduced or very reduced appendages. The ocelli and the transverse groove which are considered to have been present in the Euthycarcinidae cannot be distinguished, though they were most probably present even if only in the reduced form that occurs in Recent Anostraca.

This review of the structure of *Synaustrus* and of *Euthycarcinus* would indicate that there is a very close relationship between these fossils and the Anostraca. The main differences are associated with the development of a dorsal shield on the head and thorax and the presence of a caudal style in the Euthycarcinidae.

As far as can be ascertained the head of the Euthycarcinidae bears appendages and processes comparable with those of Anostraca, even to the development of sexual dimorphism in the second antennae. The main differences are apparently associated with the development of a dorsal head shield in the Euthycarcinidae and its great reduction in Anostraca. As the head shield was reduced in the Anostraca it is suggested that the eyes retained their lateral position and became stalked.

The trunk of the Euthycarcinidae can be compared with that group of Anostraca in which there are eleven appendage-bearing trunk segments. The major difference between the two lies in the development of a five-partite dorsal shield in the Euthycarcinidae and its absence in Anostraca. The trunk is considered to be twelve-segmented in the Euthycarcinidae. This twelfth segment is without appendages, but dorsally it is incorporated in the dorsal shield. It constitutes the genital segment. Dorsally it remains simple but ventrally there appears to be a difference between the sexes. In the female it is partly divided to form a brood-pouch but no division is obvious in the male. The genital segment is partly subdivided in the Anostraca, where it is regarded as the first abdominal segment.

The abdomen of the Euthycarcinidae differs quite noticeably from that of the Anostraca. In the Euthycarcinidae it consists of four simple segments and a long caudal style but in the Anostraca, if one excludes the genital segment and its subdivision, there are seven apparent segments and the terminal segment is without a caudal style but is produced laterally to form the furca. It is suggested that each of the first three abdominal segments of the Euthycarcinidae is most probably represented in the Anostraca by a divided segment comparable with the division which has occurred in the genital segment.

The changes in interpretation of *Synaustrus brookvalensis* that are required in the light of the structure which in all probability occurs in *Euthycarcinus* are expressed in new reconstructions of both dorsal and ventral surfaces (figure 2) which differ from the original composite reconstruction mainly in the interpretation of the head tagma.

Systematic Position of the Euthycarcinidae

There has been marked difference of opinion on the systematic position of the Euthycarcinidae within the Arthropoda. Handlirsch (1914) placed *Euthycarcinus kessleri* Handlirsch in the Crustacea and made it the basis of a new order, Archicopepoda, allied to the Copepoda. The reconstruction given by Handlirsch showed a body consisting of only a small number of segments, and the caudal extremity was illustrated as ending in two long furcal lobes. The appendages were considered to be biramous. Restudy of the species by Gall and Grauvogel (1964), based on additional well preserved specimens, has shown a very different structure, with the body consisting of a much larger number of segments and ending in a single caudal style. Also, the appendages were interpreted as simple and not biramous. Gall and Grauvogel remarked on the unusual combination of characters possessed by this species and compared it with the merostomes on the presence of a long caudal style and the Diplopoda on the structure of the dorsal shield and also with such forms as *Emeraldella* amongst the Trilobitomorpha but considered that the segmentation of the body, the conformation of the cephalic appendages and the absence of intestinal diverticulae establish a certain Crustacean affinity. However, they consider that the unusual combination of characters necessitate the establishment of a new subclass, Euthycarcinoidea, with affinities to both the Branchiopoda and the Cephalocarida, and thus agreed with Handlirsch only to the extent of placing the fossil species in the class Crustacea. Riek (1964) placed *Synaustrus brookvalensis* in the class Trilobitoidea to a large extent on the presumed simple structure of the head tagma, and on the development of a long caudal style. The re-interpretation of the structure of the head tagma shows that the species is closely related to the Anostraca (Crustacea).

Although the Euthycarcinidae have been shown to be closely related to the Anostraca, the differences are such that the family is best considered to form the basis of a separate subclass, Euthycarcinoidea, within the Branchiopoda.

Subclass Euthycarcinoidea

Diagnosis.—Body form similar to that of the Anostraca apart from a broad dorsal shield on the head, a broad five-partite dorsal shield on the thorax with each section of the dorsal shield formed by fusion between either two or three tergites and the abdomen ending in a long caudal style. Head large; eyes sessile, situated almost at the lateral margin; first antenna inconspicuous; second antenna large, sexual dimorphism marked. Thorax twelve-segmented, with the first eleven segments

bearing paired appendages consisting of a number of simple segments, appendages appearing uniramous; twelfth thoracic segment forming the genital segment, with a well developed brood-pouch in the female. Abdomen consisting of four simple segments and ending in a long caudal style. Intestine a simple, straight tube.

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NOTES ON THE TAXONOMY AND ZOOGEOGRAPHY OF THE TASMANIAN GRAPSID AND OCYPODID CRABS (CRUSTACEA, BRACHYURA)

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Figures 1–10

Manuscript received, 19th March, 1968

ABSTRACT

Seven of the eleven species of shore crabs of the families Grapsidae and Ocypodidae occurring in Tasmania are considered; synonymies, detailed locality lists and comments on previous work are given; the remaining four species have been recently discussed in detail elsewhere by Campbell and Griffin (1966). The sesarmine *Paragrapsus laevis* (Dana) is recorded definitely from Tasmania for the first time. The status of this species and of *Leptograpsodes octodentatus* (H. Milne Edwards) is discussed. The zoogeographical relations of the Tasmanian grapsid and ocypodid fauna are considered.

INTRODUCTION

Until recently, ten species of shore crab belonging to the families Grapsidae and Ocypodidae were considered to be present in Tasmania. Except for two widespread species, the majority of these were described by the French carcinologist H. Milne Edwards around the middle of last century. Previous Australian monographs on Crustacea (Haswell, 1882b; Hale, 1927a) had dealt briefly with most of these, M. W. F. Tweedie (1942) had treated the Tasmanian species in more detail, whilst Guiler (1952a, 1956) gave additional distributional data. Recently, Campbell and Griffin (1966) have given detailed revisions of those species belonging to the subfamily Sesarminae. The included Tasmanian species were *Cyclograpsus granulosus*, *Helograpsus haswellianus*, *Paragrapsus quadridentatus*, and *P. gaimardii*. In the present paper the taxonomy of these species is not further considered. Another species dealt with by Campbell and Griffin was *Paragrapsus laevis*. The evidence they had available then suggested that this species probably does not occur in Tasmania, but in the present paper it is recorded from a few localities on the central east coast and one on the north coast; the taxonomic status of these populations is discussed.

As Campbell and Griffin (1966: 141) noted, the grapsid described by Jacquinot (in Jacquinot and Lucas, 1853) from "Hobart", *Cyclograpsus tasmanicus*, cannot be identified with any known species of *Cyclograpsus* or with any Tasmanian crab, and its status must remain uncertain for the present. During the course of the studies reported in part here, the status of two geographically widespread species, *Leptograpsus variegatus* and *Plagusia chabrus*, were investigated throughout their range. The results of these studies will be given in detail elsewhere and the two species are only briefly dealt with here.

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Dr R. W. George has recently completed a study of the species previously known as *Brachynotus octodentatus* and has considered that it should be placed in the genus *Leptograpsodes*. This placing is followed here, and George's studies are commented upon.

In the present paper, then, brief notes are given on five of the nine species of Tasmanian grapsids and the two species of ocypodid. Except in the case of the two widespread species mentioned above, and of *Paragrapsus laevis*, full synonymies are given. All Tasmanian localities at which each species is known to occur are listed and those important morphological features not previously mentioned in the literature are described. The taxonomic status of *Leptograpsodes octodentatus*, *Brachynotus spinosus*, and *Paragrapsus laevis* is discussed. Finally, the zoogeographical relations of the Tasmanian grapsid and ocypodid fauna are considered.

Terminology used here follows that used by Campbell and Griffin (1966) and by Rathbun in her various publications. Dimensions given are carapace widths in mm as measured with vernier or dial calipers.

The material on which this study was based has been deposited in the Tasmanian Museum, Hobart; Queen Victoria Museum, Launceston; Australian Museum, Sydney; Dominion Museum, Wellington; and U.S. National Museum, Washington.

TAXONOMY

Family **GRAPSIDAE**

Subfamily **GRAPSINAE**

Genus **Leptograpsus** H. Milne Edwards, 1853

Leptograpsus variegatus (Fabricius)

Restricted synonymy:

Cancer variegatus Fabricius, 1793: 450.

Leptograpsus variegatus; Tweedie, 1942: 14. Guiler, 1952a: 40. Guiler, in Guiler, Serventy and Willis, 1958: 182. Bennett, 1964: 80.

Material examined.—A total of 20 specimens (12 ♂♂, 8 ♀♀, 21–75 mm).

Localities.—Bass Strait: Citadel I., Glennie Gp.; Currie Harb., King I. Tasmania: Eddystone Pt.; Binnalong B.; Bicheno; Coles B.; C. Forestier; Maria I.; Pirates B. (see fig. 8).

Habitat.—On rocky coasts exposed to strong surf, sheltering in crevices around high tide mark and wandering over surface of the rocks and in pools.

Distribution.—Southern warm temperate Indian and Pacific Oceans from Shark Bay, Western Australia, through southern and eastern Australia and New Zealand to Chile in South America.

Remarks.—Bennett and Pope in their survey of intertidal zonation in Tasmania (Bennett and Pope, 1960) found this species along the east coast at Swan Island, Sleepy Bay, Fossil Island at Pirates Bay and the Remarkables Cave (Elizabeth C. Pope, pers. comm.). This species is found in quite large numbers in some localities in Tasmania but, apart from the mention of it given by Bennett and Pope, has not been previously recorded from Tasmania. Guiler (in Guiler, Serventy and Willis, 1958) recorded this species from Fisher Island, just to the south of Flinders Island.

As will be shown in a future paper, Western Australian, New Zealand, and South American populations form a single specific unit taxonomically, as previously reported by Rathbun (1918), Garth (1957), and Bennett (1964).

Genus **Leptograpsodes** Montgomery, 1931

Leptograpsodes octodentatus (H. Milne Edwards)

Figs. 1, 2a-c, 3a

Cyclograpsus octodentatus H. Milne Edwards, 1837: 80 (type locality: King I., Bass Strait; type in Muséum National d'Histoire Naturelle, Paris—*vide* Montgomery, 1931).

Heterograpsus octodentatus; H. Milne Edwards, 1853: 194. Kingsley, 1880: 209. Haswell, 1882b: 101.

Brachynotus octodentatus; Tesch, 1918: 106 (in key). Hale, 1924: 69; 1927a: 182, fig. 183; 1927b: 312. Balss, 1935: 142. Tweedie, 1942: 16, fig. 2. Guiler, 1952a: 40.

Grapsus inornatus Hess, 1865: 148, pl. vi fig. II (type locality: Sydney; type in Gottingen Museum—*vide* Montgomery, 1931). De Man, 1887: 699.

Leptograpsodes webbaysi Montgomery, 1931: 452, pl. 25 fig. 5, pl. 28 fig. 1, 1a, 1b (type locality: Long Island, Abrolhos Islands; types not extant, lost in transit— *vide* Montgomery, 1931).

Leptograpsodes octodentatus; George, 1962: 71.

Material examined.—A total of 59 specimens (30 ♂♂, 29 ♀♀, 11–35 mm).

Localities.—Bass Strait: King I.; Hunter I.; Goose I.; Chapel I. Tasmania: Just W. of Crayfish Ck.; Rocky C.; Hawley Beach, Devonport; Green's Beach; Low Head; Waterhouse I.; Pirates B.; C. Direction; Blackman's B.; Adventure B., Bruny I.; Conical Harb. (S. of Pieman R.); just S. of Interview R.; just N. of Arthur R. (see fig. 8).

Habitat.—On boulder beaches and rocky platforms exposed to moderate surf and in sheltered bays, above high tide level, under stones or in crevices, sometimes in burrows in earth, often near freshwater seepages.

Distribution.—Restricted to Australia, from the Abrolhos Islands in the west, through South Australia, Victoria, to northwestern, northern, and eastern coasts of Tasmania; not found on the east coast of the mainland north of Victoria (F. A. McNeill, personal communication to R. W. George). George (1962) reported a total of twenty-seven localities known at that time (see fig. 9).

Description.—A detailed description of this species was given by Montgomery (1931) and a shorter one by Tweedie (1942); the synonymous *Grapsus inornatus* Hess was redescribed by De Man (1887). Additional features are as follows:

Male abdomen.—Seven-segmented, widest at the middle of the laterally convex third segment, following segments narrowing uniformly, edges weakly concave, to distal edge of sixth; seventh segment laterally strongly concave basally.

Male first pleopod.—Long, quite slender, weakly curved outwards distally, sternal surface with a moderately long groove towards medial surface ending in distal flap; lateral surface sparsely setose, medial surface with numerous setae extending from base to tip; a moderately dense tuft of setae at the tip almost concealing short, blunt, horny tip and flap on sternal surface.

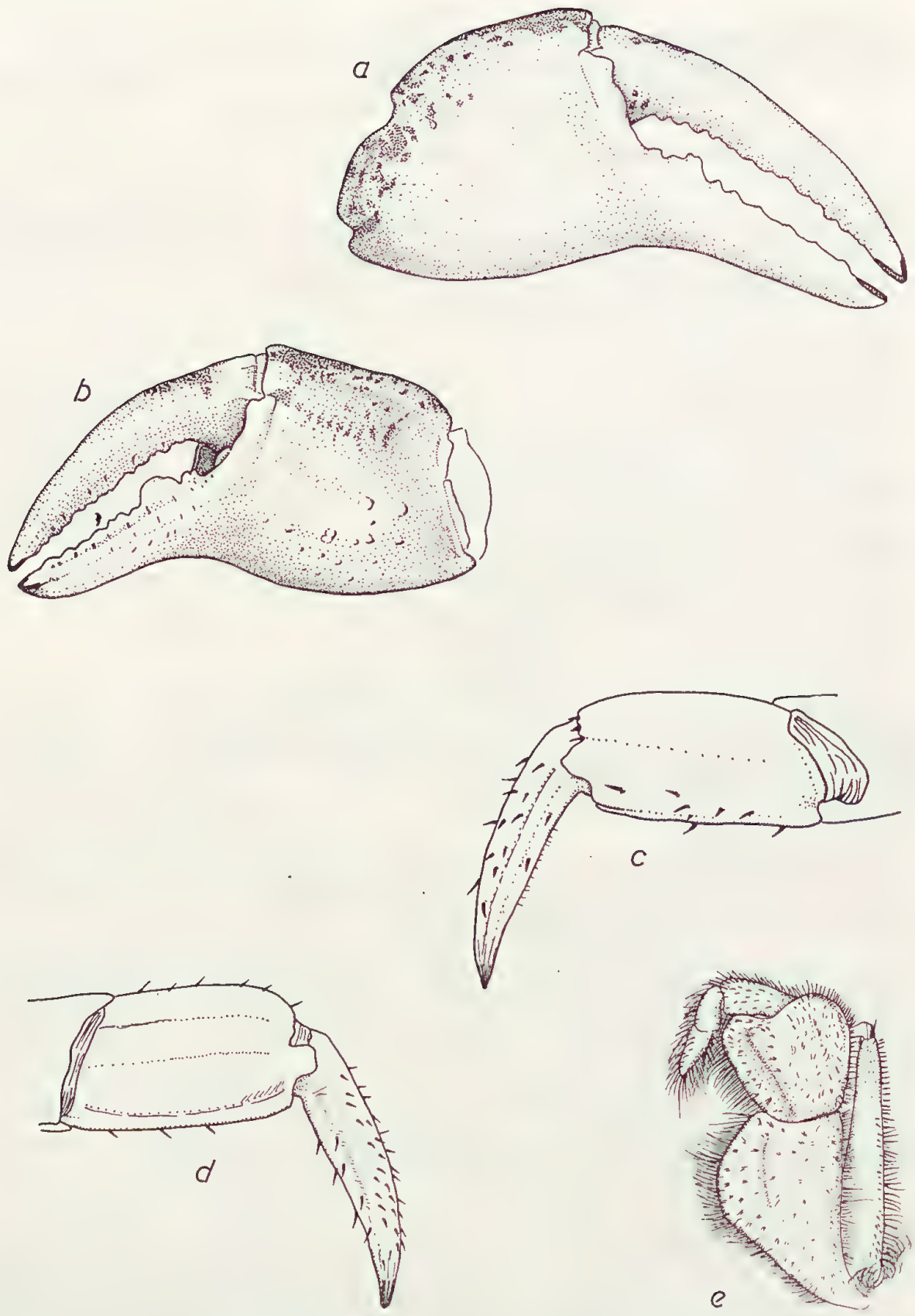

Figure 1.—*Leptograpsodes octodentatus*. Male, 33 mm, Pirates Bay: a, right chela, outer aspect; b, same, inner aspect; c, right first ambulatory leg, propodus and dactyl, anterior aspect; d, right fourth ambulatory leg, propodus and dactyl, posterior aspect; e, left third maxilliped, outer aspect.

Colour.—Olivaceous, mottled or spotted with dark brown (Tweedie). Carapace mottled with black, dark blue or purple and yellow (George). The underside of the body, the chelipeds and legs are usually much paler than the carapace, and the mottling, which occurs on the dorsal surface of the chelipeds and legs, is sometimes bright red.

Remarks.—Amongst the distinguishing characters of this species are the very strongly convex lateral borders of the carapace, the anterior half bearing three teeth behind the external orbital angle (*not* two as stated by Tweedie), the last very small; the long, outwardly smooth and inwardly sparsely tuberculate chelae with the fixed finger moderately bent from the palm; and the absence of spines from the posterior ventrodistal border of the ambulatory meri.

The carapace bears on the branchial regions, close to the lateral edge, a few weak ridges, and the suborbital spine is three-sided and only moderately large. The fingers of the chela are strongly toothed, those of the fixed finger near the base generally grouped into a strong lobe. The propodi and dactyls of the ambulatory legs bear short, stiff, black, spine-like hairs.

Montgomery (following views expressed to him by De Man) and George placed *Leptograpsodes* in the subfamily Grapsinae. However, it should be noted that *L. octodentatus* shows reasonably strong similarities to the Australian varunine *Brachynotus spinosus* (Milne Edwards) in the shape of the merus of the third maxillipeds, the appearance of the front in ventral view, especially the straight suborbital border, and in the form of the male first pleopods. The two species are quite different in the shape of the carapace and of the male chela. The presence in *L. octodentatus* of two pairs of postfrontal lobes, the strong tuberculation of the anterior part of the dorsal surface of the carapace and the presence of transverse striations on the ambulatory meri are all reminiscent of species of *Grapsus* and allied grapsines.

Montgomery realized that his *Leptograpsodes webhaysi* was very close to the species then known as *Brachynotus octodentatus*, but listed some differences between the two. Balss (1935) considered the two species almost certainly identical; the same conclusion was reached by George (1962). Hess's *Grapsus inornatus* has been considered a synonym of the present species since the time of Tesch (1918), although the type locality of the former (Sydney) is almost certainly outside the geographical range of the species (see above).

In a study of this species throughout its geographical range R. W. George examined a total of 84 specimens (50 ♂♂, 34 ♀♀, carapace width 10–70 mm). Eight characters were studied in detail by George including all those mentioned by Montgomery and De Man as delineating *L. webhaysi* and *G. inornatus* respectively. The characters concerning ridges around the orbits appear difficult to evaluate and the differences (cited by Montgomery) too slight to warrant specific separation. All other characters, including the prominence of the pits on the dorsal surface of the carapace, the dentition and shape of the fingers and ornamentation of the carpus of the cheliped are subject to significant variation with either age or sex, sometimes both. Montgomery's material (adult females), according to that author's description, agrees entirely with the typical adult females examined by George; Hess's material, according to the latter's description, does not support any taxonomic separation of eastern and western populations (George, pers. comm., December, 1962).

Examination of the Tasmanian material to hand fully supports George's conclusions; in addition to the characters already found to vary with age and sex, it appears that the ridges on the branchial regions also become less prominent with increasing overall size.

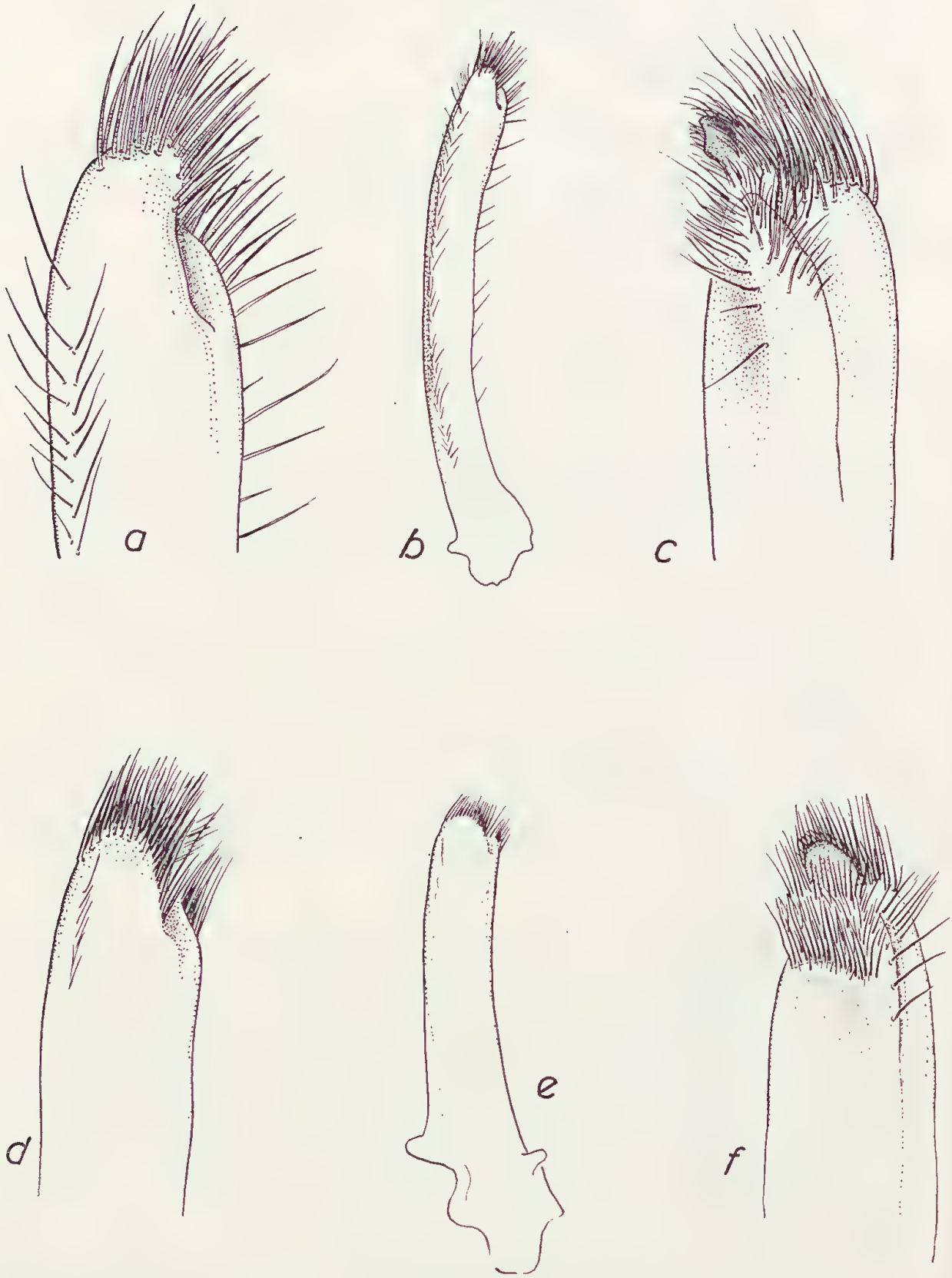

Figure 2.—Male left first pleopods of *Leptograpsodes octodentatus*, 33 mm, Pirates Bay (a-c) and *Brachynotus spinosus*, 17 mm, Pittwater (d-f): a, d, tip of pleopod, abdominal aspect; b, e, whole pleopod, abdominal aspect; c, f, tip of pleopod, sternal aspect.

Subfamily **VARUNINAE**

Genus **Brachynotus** De Haan, 1835

Brachynotus spinosus (H. Milne Edwards)

Figs. 2d-f, 3b-e

Heterograpsus spinosus H. Milne Edwards, 1853: 194. A. Milne Edwards, 1874: 82. Kingsley, 1880: 210. De Man, 1891: 56, pl. 4 fig. 15. Ortmann, 1894: 715. Fulton and Grant, 1906: 19.

Brachynotus spinosus; Tesch, 1918: 106 (in key). Tweedie, 1942: 16, fig. 3. Guiler, 1952a: 40.

Eriocheir spinosus; Hale, 1927a: 184, fig. 185; 1927b: 312, fig. 2.

Type locality.—Vanikoro, Santa Cruz, Pacific Ocean; types in Muséum National d'Histoire Naturelle, Paris—*vide* De Man, 1891.

Material examined.—A total of 62 specimens (27 ♂♂, 35 ♀♀, 6–17 mm).

Localities.—Tasmania: Detention R.; just W. of Crayfish Ck.; Triabunna; Double Ck.; Prosser R. at Orford; Carlton R.; Dunalley B.; Fort Direction; Pittwater; Bellerive Beach; Sandy B.; Howden; Margate; Oyster Cove; Huon R. at Lymington.

Habitat.—In estuaries and sheltered bays, intertidal towards high tide level, under small stones.

Distribution.—Southeastern Australia (see fig. 9), southwest Pacific Ocean.

Fulton and Grant (1906) reported this species from Port Phillip and Hale (1927b) recorded it from the Bay of Shoals and Busby Island, Kangaroo Island. Within Tasmania it was recorded from Brown's River and Carlton by Tweedie (1942) and from north of the Pieman River by Guiler (1952a). McNeill (pers. comm.) considers that Haswell's (1882) record of *Leptograpsodes octodentatus* (as *Heterograpsus octodentatus*) from the north coast of Tasmania was based on a specimen of the present species. De Man recorded this species from Upolu, Samoa.

Description.—Good descriptions of this species were given by De Man (1891) and Tweedie (1942). Additional features are as follows:

Abdomen.—Seven segmented, in the male widest towards distal edge of laterally convex third segment, following segments smoothly tapering to close to distal edge of sixth which narrows abruptly, seventh segment much narrower than sixth. Fifth segment markedly concave laterally.

Male first pleopod.—Moderately stout and hardly tapering; short groove on sternal surface towards lateral surface ending in definite flap; strong tufts of hairs, confined to distal part of the pleopod, borne towards tip of flap and surrounding horny tip of pleopod; a few short hairs extending a little way down abdominal surface somewhat medially.

Colour.—Dull green or brown with or without white markings, which may be so extensive as largely or wholly to replace the colour (Tweedie). Innumerable colour variations occur; some examples are green, others different shades of brown. Some are very dark brown, with large or small white markings, while others have the whole upper surface of the carapace milk-white (Hale, 1927a). Hale's remarks apply quite satisfactorily to Tasmanian populations. Banding of the legs is quite common.

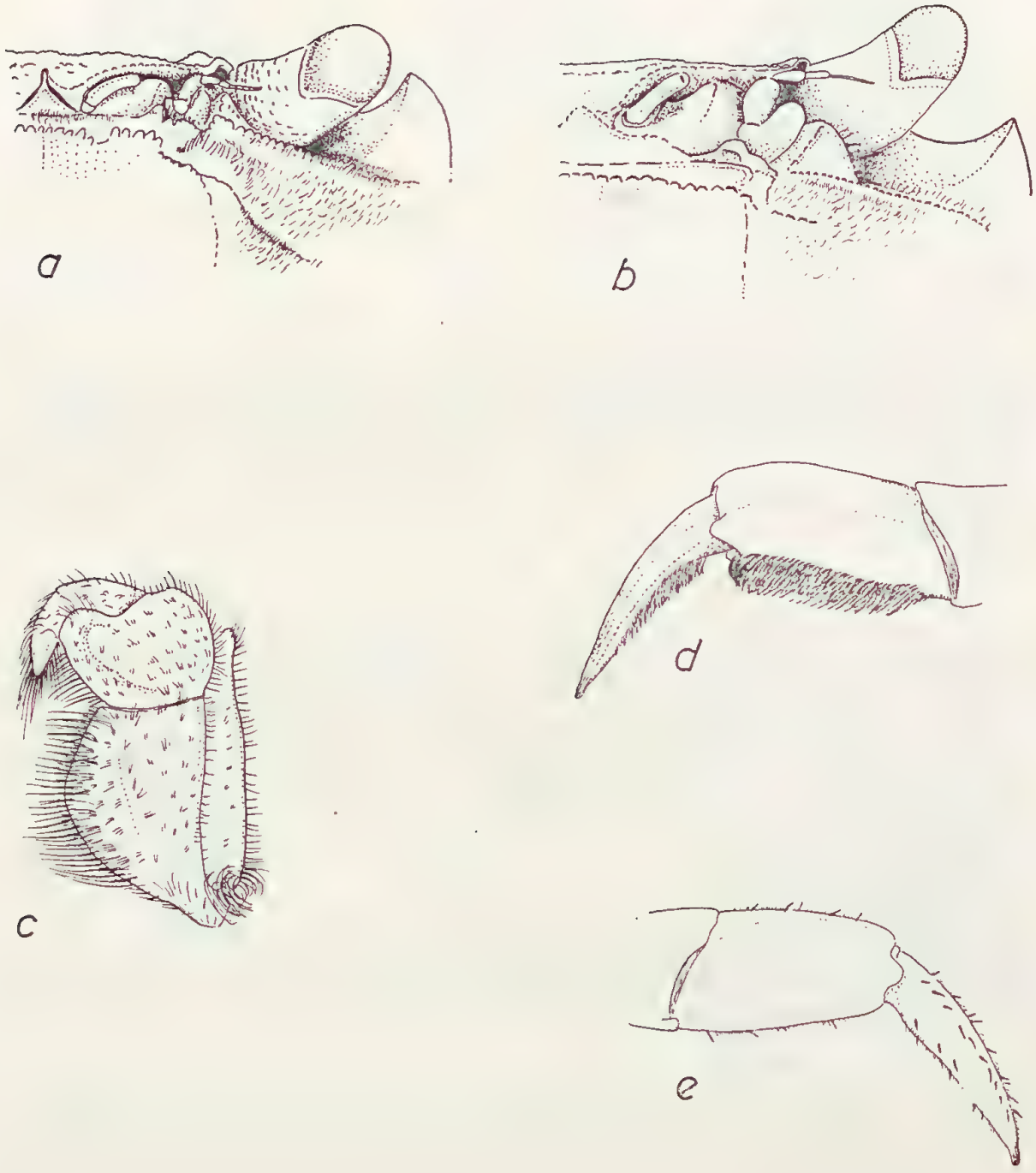

Figure 3.—*Leptograpsodes octodentatus*, male, 33 mm, Pirates Bay (a only) and *Brachynotus spinosus*, male, 17 mm, Pittwater (b-e): a, b, front of carapace and left orbit, ventral aspect; c, left third maxilliped, outer aspect; d, right first ambulatory leg, propodus and dactyl, anterior aspect; e, right fourth ambulatory leg, propodus and dactyl, posterior aspect.

Remarks.—The distinguishing characters of this species are the presence of three spines on the anterolateral margin, behind the prominent external orbital spine, the second of these smaller than the others and rounded instead of sharp, the concave front and weak postfrontal lobes, the oblique ridge from the third anterolateral spine to the posterior edge of the carapace, the large, pyramidal, three-edged, suborbital spine, the outwardly smooth and inwardly granular chelae with a strong tuft of hairs at the end of the palm between the fixed fingers on both inner and outer surfaces in males only, the presence of a strong distal dorsal spine on the ambulatory meri and stout, black, spine-like hairs distributed sparsely on the ambulatory propodi and dactyls, males also having prominent tufts of hair on the ventral surfaces of these two segments of the first ambulatories.

Tweedie (1942: 17) considered that records of this species from the tropical Pacific (De Man, 1891) required confirmation. Comparison of Tasmanian material, Tweedie's and Hale's descriptions and figures with De Man's description and figure of specimens from Samoa does not reveal to me any differences which might be regarded as warranting specific separation of Australian material from Samoan. De Man also compared his specimens with material from Australia.

Subfamily **SESARMINAE**

Only one of the five Tasmanian species belonging to this subfamily is discussed here. The remaining four, *Cyclograpsus granulosus* H. Milne Edwards, *Helograpsus haswellianus* (Whitelegge), *Paragrapsus quadridentatus* (H. Milne Edwards), and *P. gairmardii* (H. Milne Edwards) are treated in detail by Campbell and Griffin (1966).

Genus **Paragrapsus** H. Milne Edwards, 1853

Paragrapsus laevis (Dana)

Restricted synonymy:

Chasmagnathus laevis Dana, 1852a: 252.

Paragrapsus laevis; Campbell and Griffin, 1966: 160, 162, text-figs. 8B, 10C; pl. 22 fig. 2; pl. 23 fig. 10 (synon.).

Material examined.—A total of 68 specimens (51 ♂♂, 17 ♀♀, 5–37 mm).

Localities.—Tasmania: Kelso, Tamar R.; MacLaine's Ck.; Double Ck.; Prosser R. at Orford; Blackman B. at mouth of Bream Ck. (see fig. 8).

Habitat.—On sheltered stony beaches and in estuaries, intertidally under stones and in burrows.

Distribution.—Restricted to eastern Australia, from Moreton B. (Queensland) in the north, through Victoria to southeastern Tasmania (see fig. 9). Its presence in Tasmania is now fully confirmed; previously its existence here had been supported by only one specimen in the Australian Museum collections (AM P.7418). Campbell and Griffin (1966) listed 16 localities from which material of this species had been examined. It had previously been recorded from Western Port, Lakes Entrance, and Port Phillip in Victoria by Fulton and Grant (1906) as well as from more northern localities.

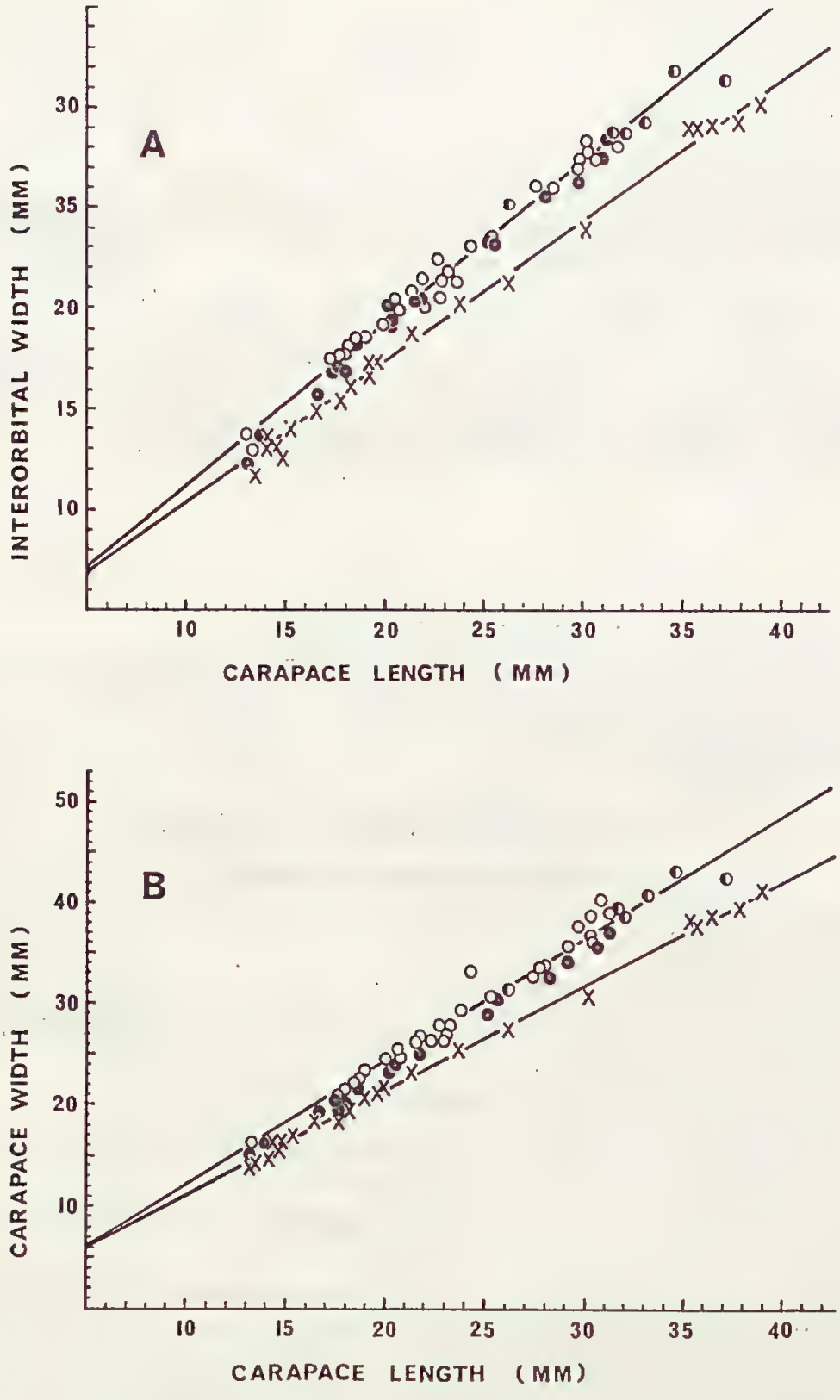

Figure 4.—Relative growth of three dimensions of the carapace in *Paragrapsus* species: A, interorbital width relative to carapace length; B, carapace width relative to carapace length. *P. laevis* (N.S.W.) are represented by open circles; *P. laevis* (Victoria) by half-closed circles; *P. laevis* (Tasmania) by closed circles and *P. gaimardii* by crosses. The lines are the regression lines fitted by the method of least squares (see text and table 1).

Remarks.—A full description of this species was given by Campbell and Griffin (1966), who dealt briefly with the differences between *P. gaimardii* and *P. laevis* and illustrated and commented upon one specimen from Victoria which appears to be intermediate between the two species in at least nine characters.

Examination of the specimens from eastern Tasmania similarly revealed at first some rather striking differences from the typical mainland specimens of this species. These differences mainly involve four characters: the felting of the propodus of the first ambulatory leg; the felting of the propodus of the fourth ambulatory leg, the nature of the junction of the first and second thoracic sternites; and the shape of the sixth segment of the male abdomen. The marked differences usually existing between the two species in these characters are set out by Campbell and Griffin (1966: 162–9).

Critical examination of seventeen of these Tasmanian specimens shows, however, on comparison with six specimens from Victoria and twenty-nine New South Wales specimens of *P. laevis* (listed in Campbell and Griffin), that there is a slight tendency for the former to have:

(1) the felt on the anterior surface of the first ambulatory propodus divided by a thin naked stripe throughout the length of the segment (2 Tasmanian, 2 Victorian, and 1 N.S.W. specimen);

(2) the felt on the dorsal surface of the fourth ambulatory propodus confined to the distal third (9 Tasmanian, 1 Victorian, and 3 N.S.W. specimens);

(3) the second sternite in the male to be raised above the first (7 Tasmanian, 5 Victorian, and 11 N.S.W. specimens);

(4) the sixth segment of the male abdomen to be twice as broad as long (see table 2).

Table 1. Relative growth of three dimensions of the carapace of *P. laevis* and *P. gaimardii* (see fig. 4); x and y are the variables given by the equation $y = a + bx$; x in all cases is carapace length. The values of a and b are given (together with their standard error) for each species and each regression. The significance given is the sums of squares due to the regression as a percentage of the total sums of squares.

Species Area (*n*)	*P. laevis* N.S.W., Victoria, and Tasmania (52)	*P. gaimardii* Victoria and Tasmania (22)
y	interorbital width	
a	2·95 (0·086)	3·28 (0·182)
b	0·81 (0·015)	0·70 (0·021)
significance	98·39	98·30
y	carapace width	
a	—0·47 (0·145)	1·10 (0·268)
b	1·22 (0·025)	1·02 (0·031)
significance	97·99	98·20

Table 2. Ratio width/length of sixth abdominal segment of males of *Paragrapsus* species.

Species	*P. laevis*			*P. gaimardii*
Area	N.S.W., Victoria, Tasmania			Victoria and Tasmania
n	29	6	17	22
Mean	1·68	1·77	1·90	2·08
s	0·070	0·110	0·112	0·096
Range	1·50–1·96	1·70–2·00	1·66–2·12	1·92–2·28

Whilst these features do represent slight differences between the two groups—in the case of the last two features there are resemblances to *P. gaimardii*—they are not consistent enough to allow any kind of taxonomic separation between Tasmanian *P. laevis* and mainland specimens. Equally, there is clear evidence that *P. gaimardii* and *P. laevis* are distinct species. The four features exhibited by the Tasmanian specimens are sometimes found in mainland ones. Tasmanian specimens show no differences from other *P. laevis* in the relative width of the carapace between the external orbital angles or more posteriorly, dimensions which differ significantly in *P. laevis* and *P. gaimardii* (see fig. 4 and table 1).

Subfamily **PLAGUSIINAE**

Genus **Plagusia** De Haan, 1835

Plagusia chabrus (Linnaeus)

Restricted synonymy:

Cancer chabrus Linnaeus, 1758: 628.

Plagusia capensis; Tweedie, 1942: 22. Guiler, 1952a, 41; 1956: 7.

Plagusia chabrus; Bennett, 1964: 85.

Material examined.—A total of 12 specimens (7 ♂♂, 5 ♀♀, 36–79 mm).

Localities.—Bass Strait: Currie Harb., King I. Tasmania: Off Stanley; Eddystone Point; Bicheno; Maria I.; Adventure B., Bruny Is.

Habitat.—On rocky coasts exposed to light to heavy surf, in crevices and pools below low tide.

Distribution.—Temperate southern Indian and Pacific Oceans from South Africa through Australia and New Zealand to Chile. Within Australia this species has been recorded from several localities in western, southern, and eastern Australia (see fig. 9). In Tasmania Guiler (1956) records the species from Pt. Puer and Port Arthur, whilst earlier Fulton and Grant (1906) and Rathbun (1923) had recorded it from Bass Strait.

Remarks.—Bennett and Pope (1960) found this species at Grant Pt., Bicheno, Sleepy Bay, C. Forestier, Fossil Island in Pirates Bay, Tasman Island, and Bruny Island (Elizabeth C. Pope, pers. comm.).

Only Guiler (see above) had previously published Tasmanian localities for this species; as in the case of *Leptograpsus variegatus*, Tweedie did not collect any specimens of *P. chabrus* from Tasmanian coasts.

Family **OCYPODIDAE**

Subfamily **OCYPODINAE**

Genus **Heloecius** Dana, 1851

Heloecius cordiformis (H. Milne Edwards)

Figs. 5a-g, 6a-c, 7a-c

Gelasimus cordiformis H. Milne Edwards, 1837: 53 (type locality: "Australasie"; type in Muséum National d'Histoire Naturelle, Paris).

Heloecius cordiformis; Dana, 1852a: 248. Hess, 1865: 144. Heller, 1874: 75. Haswell, 1882b: 91 (synon.). Whitelegge, 1889: 229. Fulton and Grant, 1906: 18. Chilton and Bennett, 1929: 762 (synon.). Tweedie, 1942: 23, fig. 9. Guiler, 1952a: 41. Guinot, 1962: 10, fig. 7a, b.

Heloecius inornatus Dana, 1852a: 248 (type locality: "New South Wales"; type probably not extant); 1852b: 321; 1855: pl. 19 fig. 7.

Heloecius areolatus Heller, 1862: 519 (type locality: "Sydney"; location of type unknown). Hess, 1865: 144.

Heloecius signatus Hess, 1865: 145 (type locality: Sydney; type in Gottingen Museum). (Not *Gelasimus signatus* Hess, 1865: 146, pl. VI fig. 6.)

Material examined.—A total of 65 specimens (38 ♂♂, 27 ♀♀, 5–25 mm).

Localities.—Tasmania: Crayfish Ck.; Swan B., Tamar R.; Double Ck.; Prosser R. at Orford; Eaglehawk B.; Risdon Cove; Elwick B.; North West B.; Margate; Snug B.

Habitat.—In muddy estuaries, intertidal, in burrows (see Griffin, 1965).

Distribution.—Confined to eastern Australia, from Brisbane R. in the north to Tasmania in the south (see fig. 10). Tweedie recorded this species from Brown's River and Orford and it has also been recorded from several eastern Australian localities.

Hess (1865: 144) recorded this species from "South Australia" under the name *Heloecius inornatus* Dana. It has not since been recorded west of Western Port, Victoria, so that its presence in South Australia should be regarded as unlikely.

Remarks.—A reasonably good description and figure of this species were provided by Tweedie (1942: 23, fig. 9).

The suborbital border bears, not far from the base, a small, sharp, slender spine. As Tweedie notes, the first three ambulatory meri are densely hairy dorsally and ventrally. However, this is true only of the males; females have all the ambulatories naked, the dorsal, anteroventral and posteroventral edges of the meri being finely tuberculate. The whole of the ventral surface of the merus of the cheliped is also densely felted in the male but naked in females. Sexes can be separated on the basis of this last character down to a carapace width of 5 mm. Females, and juveniles of both sexes, have a relatively small chela with the fingers somewhat longer than the palm.

The basal teeth of the dactyl of the cheliped are generally grouped into a prominent lamina.

Supplementary characters include the presence of more or less broad, spooned hairs on the tip of the endopodite of the second maxilliped and of "woolly" hairs on the inner edge of the merus (cf. *Uca* species—Crane, 1941).

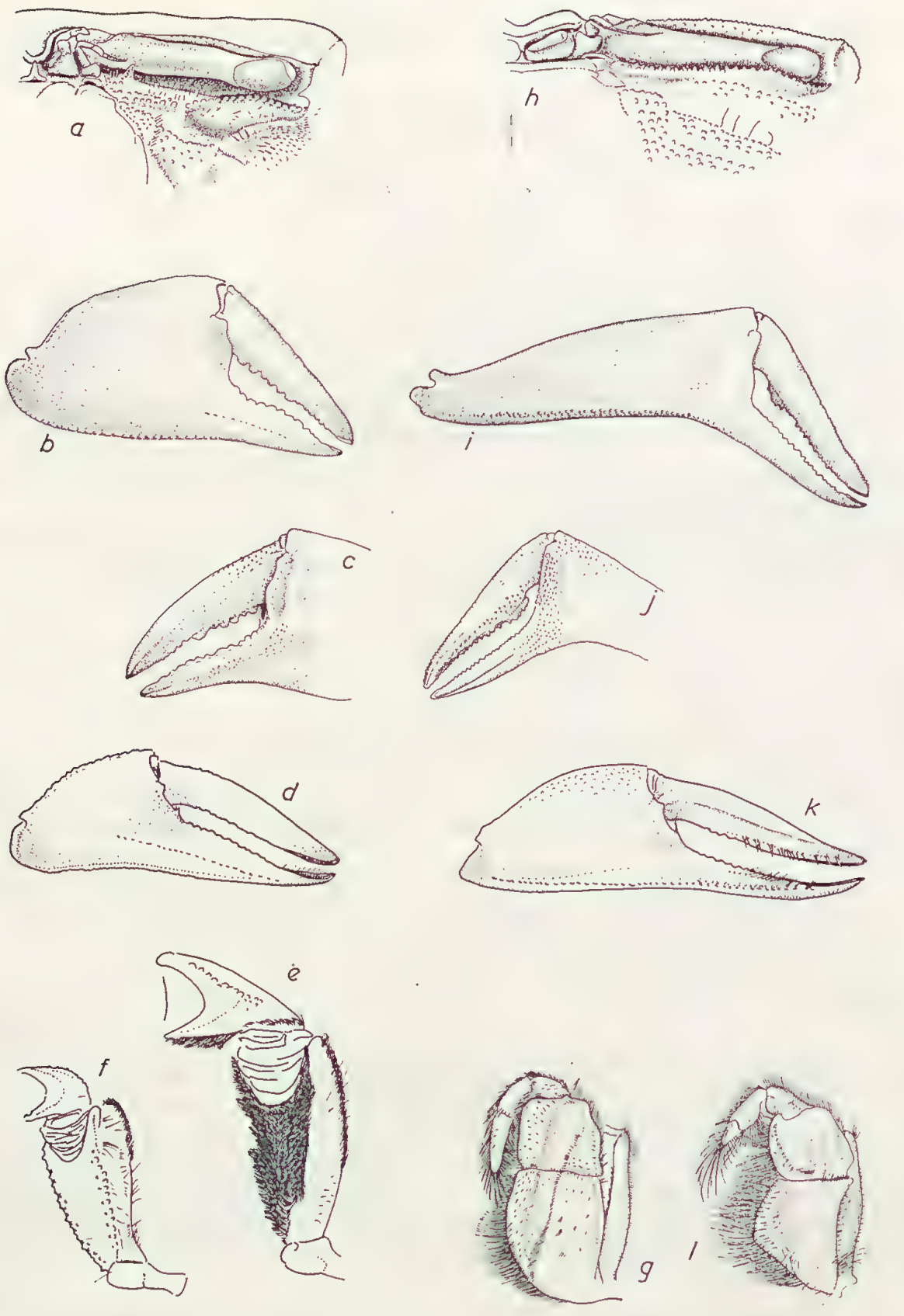

Figure 5.—*Heloecius cordiformis* (a-g), male, 22 mm, Snug Bay (a-c, e-g), female, 20 mm, Margate (d, f); and *Hemiplax latifrons* (h-l), male, 26 mm (h-j, l), female, 21 mm (k only), near Wynyard: a, h, front of carapace and left orbit, ventral aspect; b, i, male right chela, outer aspect; c, j, tip of same, inner aspect; d, k, female right chela, outer aspect; e, f, right cheliped, merus and carpus, oblique inner aspect (e, male; f, female); g, l, left third maxilliped, outer aspect.

The male first pleopod has previously been figured by Guinot (1962).

The carapace, legs, and proximal segments of the chelipeds of this species are dark greenish-blue obscurely mottled with brown, the palm of the chelae dull slate-blue, paler distally and fading to white on the fingers (Tweedie, 1942).

Subfamily **MACROPHTHALMINAE**

Genus **Hemiplax** Heller, 1865

Hemiplax latifrons (Haswell)

Figs. 5h-l; 6d, e; 7d-f

Macrophthalmus latifrons Haswell, 1882a: 549; 1882b: 90. Tesch, 1915: 154–5.

Microphthalmus latifrons; Fulton and Grant, 1906: 19 (incorrect subsequent spelling of *Macrophthalmus* Heller).

Hemiplax latifrons; Etheridge and McCulloch, 1916: 13, pl. iv figs. 4–5; pl. vi figs. 2–4. Hale, 1927a: 186, fig. 187. Tweedie, 1942: 25, fig. 10. Guiler, 1952a: 41.

Type.—Holotype, a male, carapace width 29·6 mm, a dry specimen fixed on glass with printed label "Type Macrophthalmus latifrons, Hasw. Loc. Port Phillip, Victoria" and registered as P.697; Australian Museum, Sydney. The carapace is slightly fractured, the first right ambulatory leg is missing and all the right ambulatory legs, except the first, are independently fixed to the glass.

Material examined.—A total of 77 specimens (45 ♂♂, 32 ♀♀, 8–26 mm).

Localities.—Tasmania: Wynyard; Swan B., Tamar R.; Prosser R. at Orford; Carlton R. near Carlton; Eaglehawk B.; Coal R.; Pittwater; Risdon Cove; Brown's R.; North West B.; Margate; Snug B.; Huon R. at Franklin.

Habitat.—In muddy estuaries, intertidal, in burrows (see Griffin, 1965).

Distribution.—Confined to southeastern Australia, from St Vincent's Gulf through Victoria to Tasmania (see fig. 10). This species has been reported from Orford and the Carlton River in Tasmania (Tweedie) and from a few localities in Victoria and South Australia (Fulton and Grant; Hale).

Remarks.—A reasonably good description of this species was provided by Tweedie (1942: 25, fig. 10) and it has also been figured by Hale (1927a: fig. 187).

The second to fourth ambulatory legs are densely felted in both sexes, the first leg being naked with the merus finely tuberculate along the edges.

The male pleopod bears a dense fringe of plumose setae along its lateral surface. The distal flap is almost wholly on the sternal surface and the tip bears quite a dense cluster of simple setae.

Supplementary characters include the presence of poorly expanded, deeply serrate spooned hairs on the tip of the endopodite of the second maxilliped and of simple hairs on the inner edge of the merus.

Individuals of this species are generally dark greenish or greyish brown, the chelae paler (Tweedie, 1942). The underside of the body is also pale and there may be a transverse band of pale pink across the central sternites.

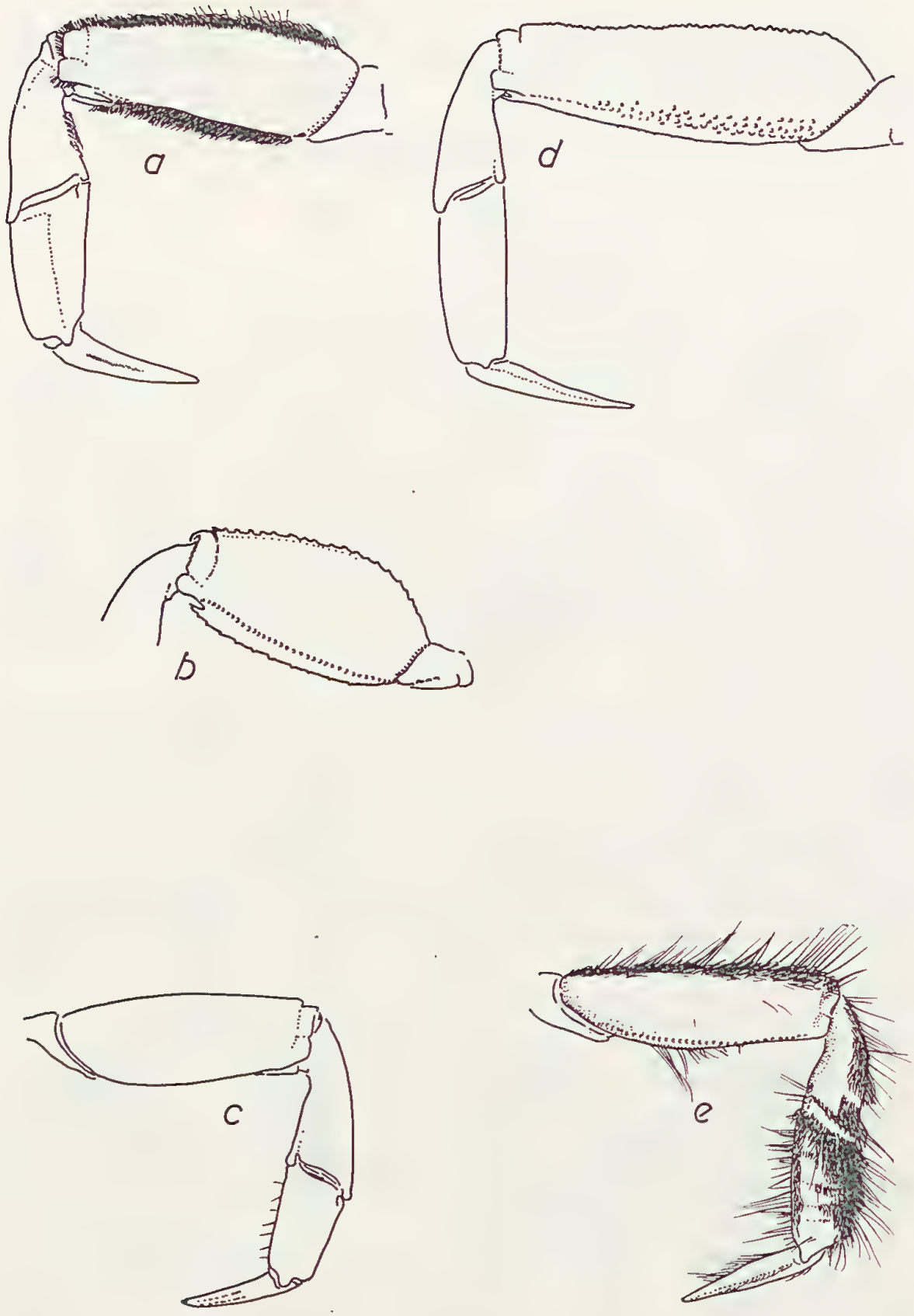

Figure 6.—*Heloecius cordiformis* (a-c) and *Hemiplax latifrons* (d-f), same specimens as in fig. 5: a, d, male right first ambulatory leg, anterior aspect; b, female right first ambulatory leg, merus, anterior aspect; c, e, male right fourth ambulatory leg, posterior aspect

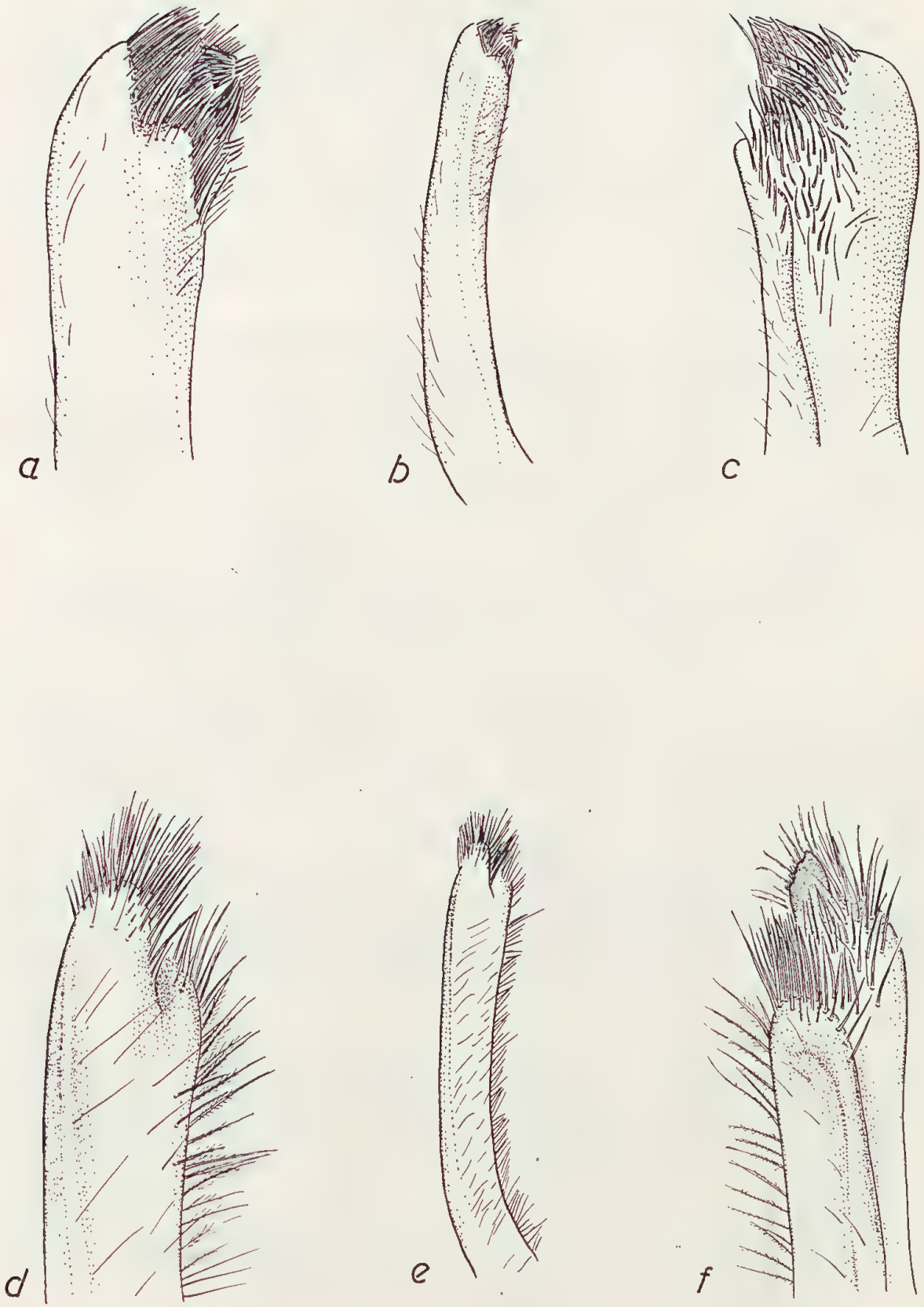

Figure 7.—Male first pleopods of *Heloecius cordiformis* (a-c) and *Hemiplax latifrons* (d-f), same specimens as in fig. 5: a, d, tip of pleopod, abdominal aspect; b, e, whole pleopod (except base), abdominal aspect; c, f, tip of pleopod, sternal aspect.

H. latifrons can be easily distinguished from the New Zealand congener *H. hirtipes* (Jacquinot) by the slightly narrower front [from a quarter to a fifth carapace width (Tweedie) as opposed to one-third carapace width in the New Zealand species—Richardson, 1949a: 36.] Examination of material of *H. hirtipes* (an adult male and female—AM P.700—in the Australian Museum's collections) show the following other differences between the two species:

(1) the eyestalks are slender and reach fully to the tip of the exorbital spine in *H. latifrons* but are stout in *H. hirtipes* and shorter, not nearly reaching the exorbital spine;

(2) the carapace widens markedly posteriorly in *H. latifrons* but narrows in *H. hirtipes;*

(3) the anterolateral margin bears two broad, rounded lobes behind the orbit in *H. latifrons* and two sharp flattened spines, in *H. hirtipes;*

(4) the carpus of the cheliped is long and slender in *H. latifrons* without a spine but short and fairly stout in *H. hirtipes* with a dorsal spine on the inner surface.

The relationship of *H. latifrons* to species of *Macrophthalmus* requires further elucidation in view of these strong differences from *H. hirtipes.*

ZOOGEOGRAPHY AND RELATIONSHIPS OF THE TASMANIAN GRAPSID AND OCYPODID FAUNA

Of the eleven Tasmanian grapsids and ocypodids, all but two are widely distributed around Tasmania. These two are *Leptograpsus variegatus* and *Paragrapsus laevis*, which appear to be confined to the northern part of the east coast, perhaps due to the influence of the warm East Australian current. Previously, *L. octodentatus* has been reported only from the north coast. This species is, however, quite widely distributed around Tasmania.

None of the species is confined to Tasmania. However, five species are otherwise known only from Victoria and eastern South Australia. These are *C. granulosus*, *P. quadridentatus*, *P. gaimardii*, and *H. latifrons*, which are endemic to Australia, and *B. spinosus*, which is known also from two localities in the central-west Pacific Ocean. The distributional limits of these species are additional evidence for the existence of the southeastern Australian "Maugean" marine province (Bennett and Pope, 1953, 1960).

Of the remaining six species, three (*H. haswellianus*, *P. laevis*, and *H. cordiformis*) have an eastern distribution in Australia, being known from as far north as Brisbane (Queensland) and along Victorian coasts; the distribution of *H. haswellianus* also includes South Australia. Of those species which occur outside Victoria and South Australia, *L. octodentatus* is the only one which is not known from central eastern Australia. The distribution of this species is western; it is not known outside Australia.

Two species only, *L. variegatus* and *P. chabrus*, are widespread outside Australia. Within Australia, both species are widely distributed southern forms.

The distribution patterns of the eleven are compared in table 3; text-figure 8 shows the Tasmanian distribution of four species, the two with limited eastern distributions and two with wider distributions. Text-figures 9 and 10 show the Australian distributions of all species.

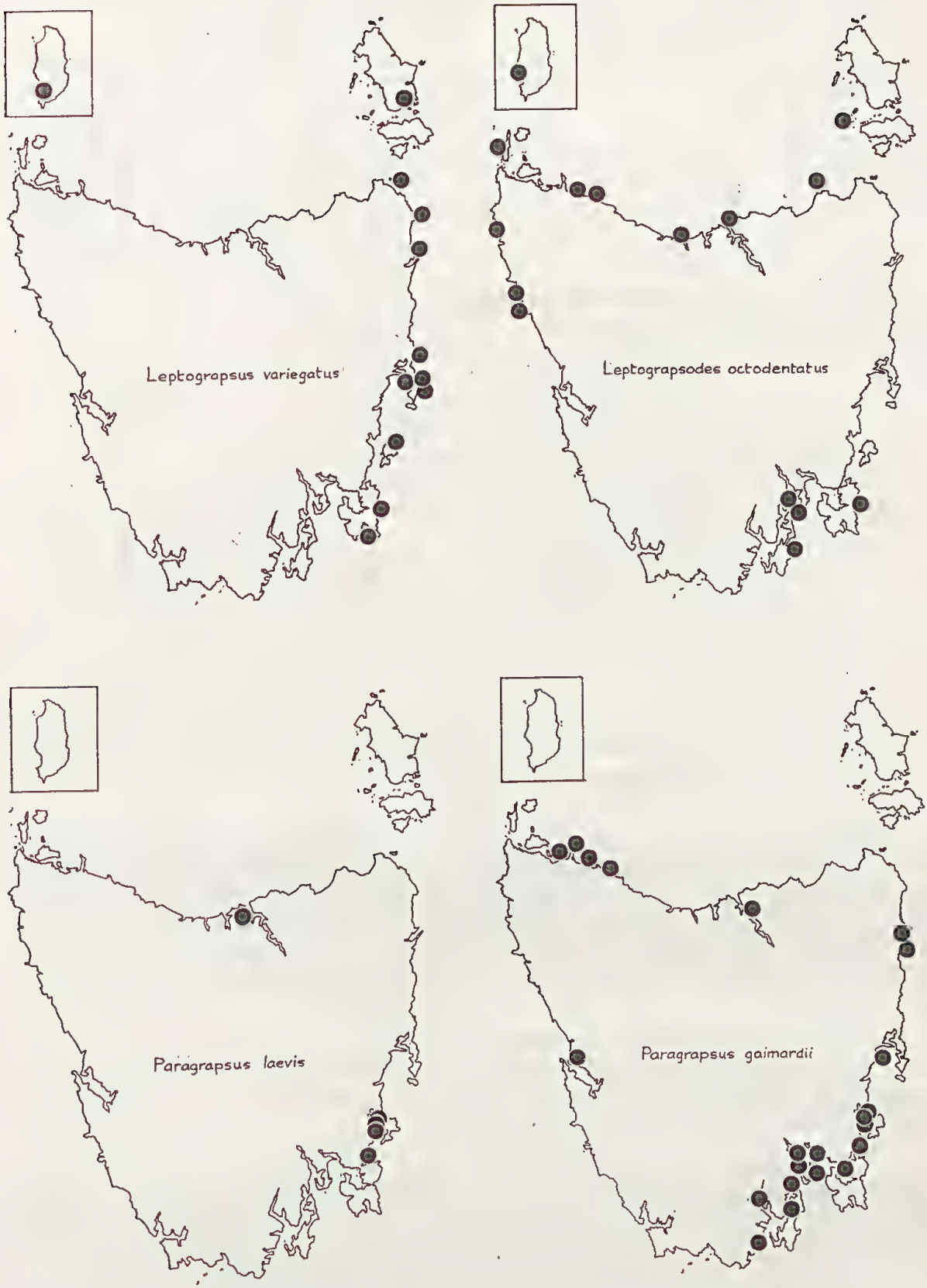

Figure 8.—Known Tasmanian distribution of four species of Grapsidae. As far as possible each circle represents a single locality.

Table 3. Geographical distribution throughout Australia and the southern Indo-Pacific of the eleven species of Tasmanian Grapsidae and Ocypodidae.

South Africa	N.W. Australia[1]	S.W. Australia[2]	South Australia		Victoria	New South Wales	Queensland	Western Pacific[3]	New Zealand	Eastern Pacific[4]	Chile
	X	X	X	Leptograpsus variegatus ..		X	X	X	X	X	X
		X	X	Leptograpsodes octodentatus.	X						
			X	Brachynotus spinosus ..	X						
			X	Cyclograpsus granulosus ..	X						
			X	Helograpsus haswellianus..	X	X	X				
			X	Paragrapsus quadridentatus	X						
			X	Paragrapsus gaimardii ..	X						
				Paragrapsus laevis ..	X	X	X				
X		X	X	Plagusia chabrus	X	X		X	X		X
				Heloecius cordiformis ..	X	X	X				
			X	Hemiplax latifrons ..	X						

[1] Western Australia north of the Abrolhos Islands.

[2] Remainder of Western Australia.

[3] Pacific Ocean west of Tuamotu Archipelago, excluding New Zealand.

[4] Pacific Ocean east of Tuamotu Archipelago.

The eleven Tasmanian species are at present included in nine genera. Four of these, *Leptograpsodes*, *Helograpsus*, and *Heloecius*, which are monotypic, and *Paragrapsus*, which contains three species, are restricted to Australia, and one *Hemiplax*, which contains one other species, is represented only in New Zealand and perhaps the south Pacific. The genera *Brachynotus*, *Cyclograpsus*, and *Plagusia*, all containing fairly large numbers of species, are widely represented throughout the Indo-west-Pacific.

Lastly, the monotypic *Leptograpsus* is a widely distributed, southern warm temperate genus. Thus, of the five genera found outside Australia three are widespread Indo-west-Pacific taxa and four are represented in other temperate regions including New Zealand.

Of the grapsid subfamilies, the best represented is the Sesarminae with five species and three genera; the other subfamilies are each represented by one or two species and genera.

The relationships of the Tasmanian (and southeastern Australian in general) grapsid and ocypodid fauna are clearly with the rest of Australia and the Indo-west-Pacific. There, the local species and genera find their closest relatives if they are not actually present themselves. Certainly, there are similarities with other non-Australian cool temperate regions, particularly New Zealand, such as the sharing

Figure 9.—Known geographical distribution, within Australia, of the nine species of Tasmanian Grapsidae. In the case of *Plagusia*, *Cyclograpsus*, and *Paragrapsus* species the distribution of one congener (*P. dentipes*, *C. audouinii*, and *P. laevis*) is shown by open, instead of filled, circles. As far as possible each circle represents a single locality; distribution of *Leptograpsodes octodentatus* after George (1962).

of the species *L. variegatus* and *P. chabrus* and of the genera *Cyclograpsus* and *Hemiplax*. Numerous similarities between the distribution patterns of southern temperate intertidal floras and faunas have been reviewed by Guiler (1952c), Knox (1960, 1963), and others. However, New Zealand, which, like Tasmania, possesses few grapsids and ocypodids (Bennett, 1964), differs notably from Tasmania in the dominance of many of its shores by varunines of the genus *Hemigrapsus*, not by sesarmines. The New Zealand species of this genus are markedly different from the Tasmanian varunine *Brachynotus spinosus*. It is doubtful, too, if the Australian *Hemiplax latifrons* is more closely related to the New Zealand *H. hirtipes* than to species of the Indo-Pacific genus *Macrophthalmus*, which is well represented on warm temperate to tropical Australian shores.

Chile (Garth, 1957) shares two species with Tasmania (see table 1) and, apart from this, one genus, *Cyclograpsus*. The two species of the latter genus are quite different from Australasian species, one, *C. punctatus*, being found also in South Africa, which possesses one species in common with Tasmania. Both Chile and South Africa (Barnard, 1950) possess varunines rather different from Tasmanian ones (species of *Crytograpsus*, *Hemigrapsus*, and *Aratus* in Chile and of *Varuna* in South Africa). The similarities of the grapsid faunas of southern temperate regions due to sharing of *L. variegatus* and *P. chabrus* may be accounted for by the possible existence in these species of relatively long-living larvae, widely travelling by means of the West Wind Drift. The Tasmanian grapsids and ocypodids appear to show similar patterns in their geographic distributions and relationships to those of other Australian Brachyura (e.g., portunid crabs—Stephenson, 1962; majid crabs—Griffin, 1966).

Figure 10.—Known geographical distribution of the two species of Tasmanian Ocypodidae.

ACKNOWLEDGEMENTS

The studies reported here were carried out at the University of Tasmania and were financed by research grants to that university; this report formed part of a thesis submitted in fulfilment of the requirements for the degree of Ph.D. at the University of Tasmania, and I wish to thank Dr E. R. Guiler for his supervision of the research. I also would like to express my appreciation to Dr J. C. Yaldwyn (Australian Museum) and Emeritus Professor V. V. Hickman (University of Tasmania) for commenting on the manuscript; Dr R. W. George (Western Australian Museum) for allowing me to include here a summary of the previously unpublished results of his study of *Leptograpsodes octodentatus;* Mr B. M. Campbell (Queensland Museum) for helpful discussion; Mrs Julia Greenhill (Tasmanian Museum, Hobart) and Mr R. H. Green (Queen Victoria Museum, Launceston), for kindly allowing me to examine collections under their care, and Miss Elizabeth C. Pope (Australian Museum) for her kindness in allowing me to consult original, partly unpublished, data on the distribution of some of these species.

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ADDENDUM

Since this paper was written Griffin (*Crustaceana* 15 : 210–213, 1968) has designated the lectotype of *Plagusia capensis* De Haan, 1835, as the neotype of *Cancer chabrus* Linnaeus, 1758.

Barnes (*Trans. zool. Soc. Lond.* 31 : 239, 1968) has returned *Hemiplax latifrons* (Haswell,) to the genus *Macrophthalmus* and created for it the new subgenus (*Tasmanoplax. Hemiplax hirtipes* (Jacquinot) has been transferred to *Macrophthalmus*, *Hemiplax* being considered as a subgenus.

V. C. N. Blight, Government Printer, New South Wales—1969

SWIMMING CRABS (CRUSTACEA, DECAPODA, PORTUNIDAE) FROM ONE TREE ISLAND, CAPRICORN GROUP, QUEENSLAND

By D. J. G. Griffin

Australian Museum, Sydney

Plates 47–49. Figure 1. Manuscript received, 16th April, 1968

Two species of portunid swimming crab, *Charybdis* (*Goniosupradens*) *obtusifrons* Leene and *Thalamitoides quadridens* A. Milne Edwards, are recorded from Australia for the first time and a species of *Portunus* considered to belong to *P. longispinosus* (Dana) is recorded from Australia for the second time; the status of Australian specimens of this species is discussed. The ecological distribution on One Tree Island of these three species and eight other portunids collected in 1966 and 1967 by Australian Museum expeditions is briefly discussed.

INTRODUCTION

One Tree Island forms part of the Capricorn Group straddling the Tropic of Capricorn at the outer edge of the southern part of the Great Barrier Reef (see Gillett and McNeill, 1967: pls 16, 17). During October–November, 1966, and September–October, 1967, parties from the Australian Museum led by Dr F. H. Talbot spent about 10 weeks on the island (see Talbot, 1967). The main purpose of these expeditions was to investigate several aspects of the ecology of the coral reef fishes. The opportunity was taken on both occasions to collect decapod Crustacea from the lagoon with the aid of a small triangle dredge and from various parts of the reef crest by hand; they were also taken from coral samples both inside and outside the reef and, by SCUBA diving, they were collected, along with fishes within the lagoon and from the outer face of the reef. Eleven species of portunid swimming crabs were collected by these two expeditions; three species are dealt with in detail in this report. Notes are given on the ecological distribution of the eleven species on One Tree Island.

The references for each species include the first description and the most recent accounts. The measurement given is of carapace width (c.w.) unless otherwise indicated and was taken with dial calipers; carapace length is abbreviated as c.l. Drawings were completed with the aid of a camera lucida. All specimens have been placed in the collections of the Australian Museum (A.M.).

I wish to thank Mr and Mrs D. W. Kinsey, who accompanied the 1967 expedition, for collecting several of the specimens dealt with here. I am indebted to Professor W. Stephenson (University of Queensland, Brisbane) for his advice and comments and for making available unpublished manuscripts. I am grateful to Dr J. C. Yaldwyn (Australian Museum) for reading the manuscript, and to Charles Turner (Australian Museum) and Anthony Healy for their care in taking a series of photographs of these crabs.

G71140—1

Family **PORTUNIDAE**

Subfamily **PORTUNINAE** Stephenson and Campbell, 1960

Genus **Portunus** Weber, 1795

Portunus longispinosus (Dana)

Figs 1 a, b. Pls 47, 48

Amphitrite longi-spinosa Dana, 1852a: 277–278; 1855: pl. 17 fig. 2a–c.

Portunus longispinosus; Stephenson and Campbell, 1959: 104–106, figs 2F, 3F, pl. 2 fig. 2, pls 4F, 5F.

Material: 1 ♂, c.w. 21.7 mm, c.l. 11.4 mm, lagoon, just north of western end of island, 4–20 ft, dredged, sand and shell fragments, 27th September, 1967, M. Cameron and D. J. G. Griffin (P.15770).

1 ♂, c.w. 24.3 mm, c.l. 11.7 mm, lagoon, off western side of island, 6–10 ft, dredged, sand and shell fragments, 10th October, 1967, M. Cameron and D. J. G. Griffin (P.15771).

Remarks: These two relatively very large males and the female from One Tree Island reported on by Stephenson and Rees (1968) agree with the Lord Howe Island material recorded by Stephenson and Campbell (1959) under the name *Portunus longispinosus* (Dana) in the following important features:

1, lateral frontal lobes much longer than medials and subacute;

2, last anterolateral spine in length about one quarter of the width of carapace exclusive of spines, the posterior edge weakly convex;

3, densely granular carapace, the granules round and mainly covering the numerous elevations but the groups barely discrete near the midline;

4, proximally strongly convex, distally straight, lateral borders of the penultimate segment of the abdomen;

5, weakly concave medial edge and rounded distal border of the merus of the third maxilliped; and

6, outwardly bent but distally straight first pleopod, the tip oblique, truncate and weakly flared, the lateral surface ("outer surface" of Stephenson and Campbell) with a dense array of spinules near the tip, spinules sparse elsewhere.

In addition there is precise agreement as to spines and ridges on the carpus and palm of the cheliped. There are eight or nine anterolateral spines including that forming the outer angle of the orbit, the fourth and the sixth being small or absent.

The only important differences from the Lord Howe Island material appear to be that the penultimate segment of the abdomen has the lateral margins parallel in the distal half, rather than gradually tapering or sinuous. The chelipeds are very long, ca 2.4 cl in the smaller, ca 2.7 c.l. in the larger, there are 4 or 5 spines on the anterior border of the cheliped merus, the most distal being well separated from the others; and finally, the last anterolateral spine projects backwards rather than outwards.

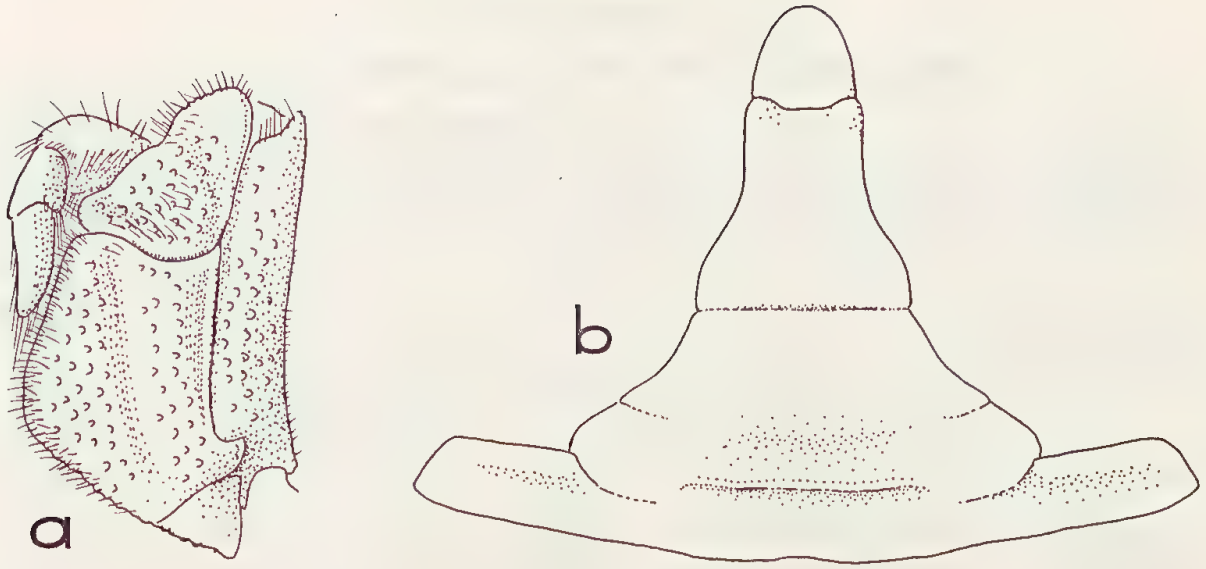

Figure 1. *Portunus longispinosus*, male, 24.3 mm, One Tree Island lagoon (AM P.15771): a, left third maxilliped; b, abdomen—segments 3–7

Until 1962 *P. longispinosus* was considered to occur throughout the Indo-west Pacific from Mauritius through New Caledonia and Fiji to Japan and Hawaii. Crosnier (1962:65), however, considered that both the Japanese and Hawaiian specimens, recorded by Sakai (1939) and by Rathbun (1906) respectively, were distinct from Dana's species. In this he was followed by Stephenson and Rees (1967: 28–31), who provided a key to the several species forming the difficult "*longispinosus* complex." Stephenson and Rees also regarded *P. longispinosus* Stephenson and Campbell as not clearly referable to Dana's species and preferred to consider the former as probably conspecific with *P. emarginatus* Stephenson and Campbell, originally recorded from northeastern Australia and now known also from Madagascar (see Crosnier, 1962: 66). Examination of the holotype of this last species shows that it differs in a number of features, which are surely reliable, from the Lord Howe Island and the present material referred to *P. longispinosus*. These include relative prominence of the lateral frontal lobes, shape of the merus of the third maxilliped, shape of the penultimate segment of the abdomen in the male and shape and ornamentation of the first pleopod in the male. The action of Stephenson and Rees thus seems unwarranted.

The apparent differences between the Lord Howe Island and One Tree Island specimens and the description and figures by Dana are small enough, allowing for some inaccuracies in Dana's figures, to permit these Australian specimens to be regarded as referable to Dana's species. The only major apparent differences concern the granulation of the carapace: this is not mentioned in the description and the carapace is shown as smooth in the figure.

The characters given in keys to distinguish the Hawaiian and Japanese forms from the others until recently regarded as *P. longispinosus* do not seem reliable enough to allow specific distinction.

Distribution: Indian and western Pacific Oceans.

Genus **Charybdis** De Haan, 1833

Charybdis (Goniosupradens) obtusifrons Leene

Pl. 49

Charybdis (Goniosupradens) obtusifrons Leene, 1936: 124, figs 11–12; 1938: 140–143, figs 85–87. Crosnier, 1962: 84–85, figs 146, 146 *bis* a–c, pl. VI fig. 2. Stephenson and Rees, 1967: 13–14.

Material: 1 ♂, 57.6 mm, outer, southern face of reef, near island, about 70 metres from reef crest, on open, gently sloping coral bottom, 9 metres, 23rd September, 1967, F. H. Talbot and party (P.15768).

1 ♀, 28.6 mm, outer, southern face of reef, near island, about 40 metres from reef crest, at seaward lip of long gutter, 4 metres, 22nd September, 1967, F. H. Talbot and party (P.15769).

Remarks: The two specimens agree in all important features with the material described in detail by Leene (1938) and by Crosnier (1962). This is particularly true of the shape of the anterior and anterolateral teeth of the carapace, the presence of ridges on the dorsal surface of the carapace and the very distinctive form of the first pleopod in the male. The basal antennal article has a short crest proximally and several tubercles distally and around the base. The sixth segment of the abdomen of the male has the lateral edges parallel except distally (see Crosnier's fig. 146 *bis* c), not slightly divergent as illustrated by Leene (fig. 8) for De Man's "*C. erythrodactyla.*" The six or more spines on the posterior border of the natatory propodus are regularly spaced in the female, in which the fourth anterolateral spine is minute, but irregularly spaced in the male.

Distribution: Indo-west Pacific from the Red Sea and Madagascar in the west through India and Melanesia to Japan (Stephenson and Rees, 1967). Previously unrecorded from Australia.

Genus **Thalamitoides** A. Milne Edwards, 1869

Thalamitoides quadridens A. Milne Edwards

Thalamitoides quadridens A. Milne Edwards, 1869: 147–149, pl. 6 figs 8–15. Crosnier, 1962: 144–145, figs 249, 251. Stephenson and Rees, 1967: 101–102, fig. 37.

Material: 1 ♂ (without pereiopods), 12.6 mm, lagoon, near island, 120 yards from southern crest of reef, in "piecrust", from dead *Acropora* coral, 20th September, 1967, F. H. Talbot and party (P.15775).

Remarks: This specimen agrees with the figure and description given by Crosnier in the very broad carapace, the four anterolateral spines decreasing in size from front to back, the first (external orbital spine) with its posterior margin serrated, the front is quadrilobate, the laterals being much the smaller and obliquely directed laterally (the anterior margin of left median frontal lobe is damaged so that it appears to be incompletely divided into two lobes), the dorsal surface possesses only frontal, mesogastric and epibranchial ridges and the basal antennal article is extremely long with a granular ridge and a group of granules proximally.

This genus has not previously been recorded from Australia.

Distribution: Indo-west Pacific: Red Sea, Madagascar, Amboina, Philippines, Marshall Islands, Johnston Island, Jaluit, Samoa, Hawaii (Stephenson and Rees, 1967).

DISCUSSION

So far eleven species of portunid swimming crab have been collected from One Tree Island by the Australian Museum expeditions in 1966 and 1967. Two species not dealt with here have been reported on by Stephenson and Rees (1968). They are *Portunus orbitosinus* Rathbun and *P. granulatus* (H. Milne Edwards). Stephenson and Rees (1967) have given the most recent account of the synonymies and distributions of the other six species not dealt with in systematic detail in the present report.

Table 1. Ecological distributions of eleven species of portunids at One Tree Island

Species	*Area* Lagoon floor	Lagoon coral	Reef crest	Outer reef slope
Caphyra rotundifrons A.M.Edw.	..	x	..	..
Portunus granulatus (H.M.Edw.)	x	..	..	..
Portunus longispinosus (Dana)	x	..	..	..
Portunus orbitosinus Rathbun	x	..	..	..
Charybdis obtusifrons Leene	..	..	..	x
Thalamita admete (Herbst)	x	..	x	..
Thalamita coerulipes Jacq. and Lucas	..	x	..	..
Thalamita integra Dana	x	..	..	..
Thalamita picta Stimpson	x	..	..	..
Thalamita stimpsoni A.M.Edw.	..	..	x	..
Thalamitoides quadridens A.M.Edw.	..	x	..	..

The habitats at One Tree Island in which these eleven species have been taken are shown in table 1. The three species of *Portunus* are confined to the open floor of the lagoon whilst three species of *Thalamita* are also found on the lagoon floor. One of these, *T. admete*, is also found on the reef crest where *Thalamita stimpsoni* is one of the most abundant crabs [the other two abundant crabs of the intertidal area are the xanthid *Eriphia sebana* (Shaw and Nodder) and the grapsid *Grapsus albolineatus* Lamarck, both of which are common on beach rock] (see also Ward, 1928). *T. coerulipes* appears to be the common portunid inhabiting coral heads; *Caphyra rotundifrons* is found amongst the green algae, *Chlorodesmis comosa*, growing in small crevices in the coral heads. The dominant crabs of coral heads are, however, xanthids. This situation appears equally true for both the area inside the reef crest and the outer reef slope. The discovery in the lagoon of two such closely similar species as *Portunus orbitosinus* and *P. granulatus* and the finding of *Thalamitoides quadridens* in the coral just inside the lagoon make the One Tree Island portunid fauna worth further investigation. Finally, it is clear that the collections to date have taken only a few of the portunids from this area if the fauna is in any way similar to that of the rest of the Capricorn Group (see papers by Stephenson and co-workers).

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EXPLANATION OF PLATES

Plate 47. *Portunus longispinosus*. Male, 24.3 mm, One Tree Island lagoon, 10th October, 1967 (P.15771). Photograph: Charles Turner.

Plate 48. *Portunus longispinosus*. Male, 24.3 mm (P.15771), carapace showing detail of granulation. Photograph: Anthony Healy.

Plate 49. *Charybdis obtusifrons*. Male, 57.6 mm, One Tree Island reef, 23rd September, 1967 (P.15768). Photograph: Anthony Healy.

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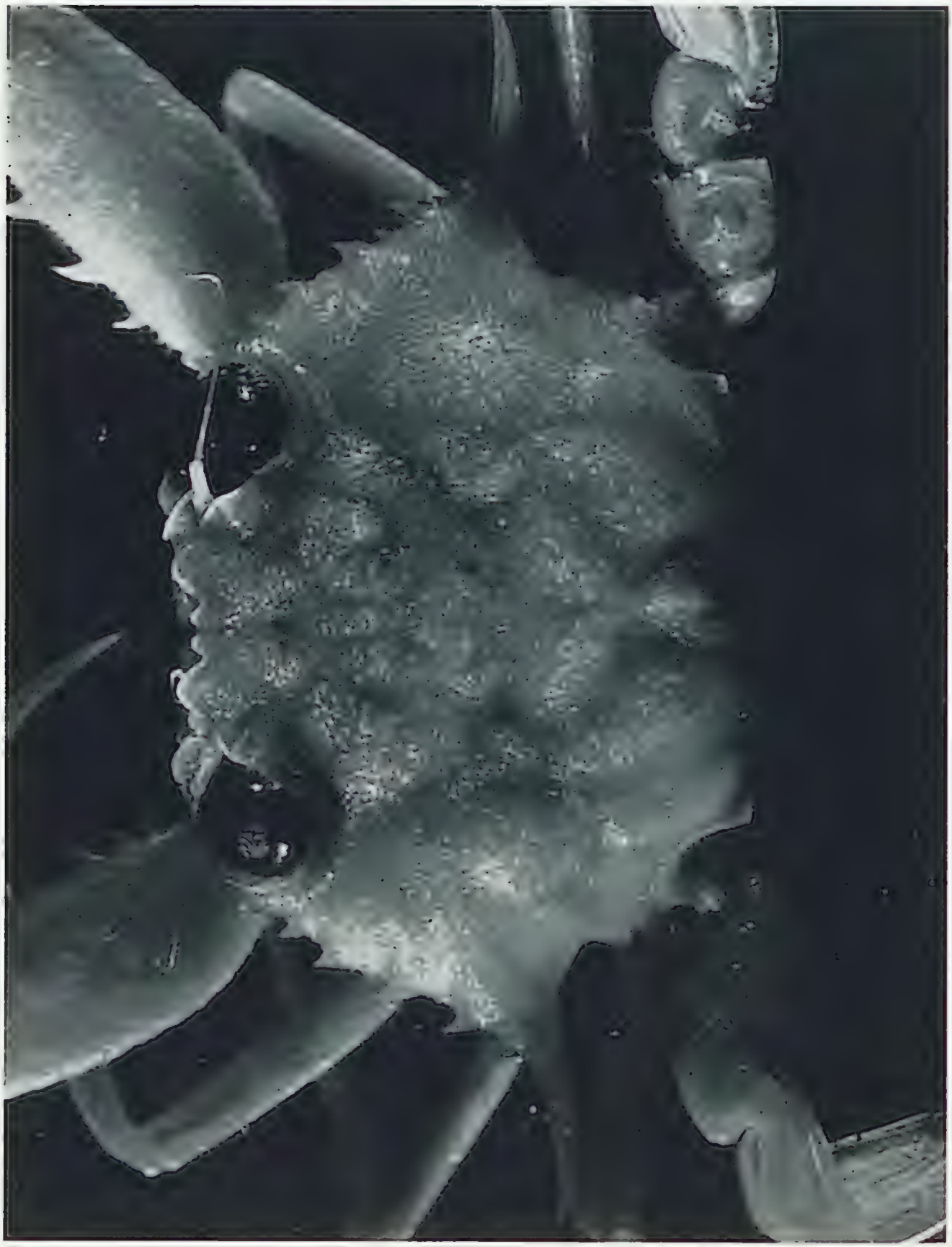

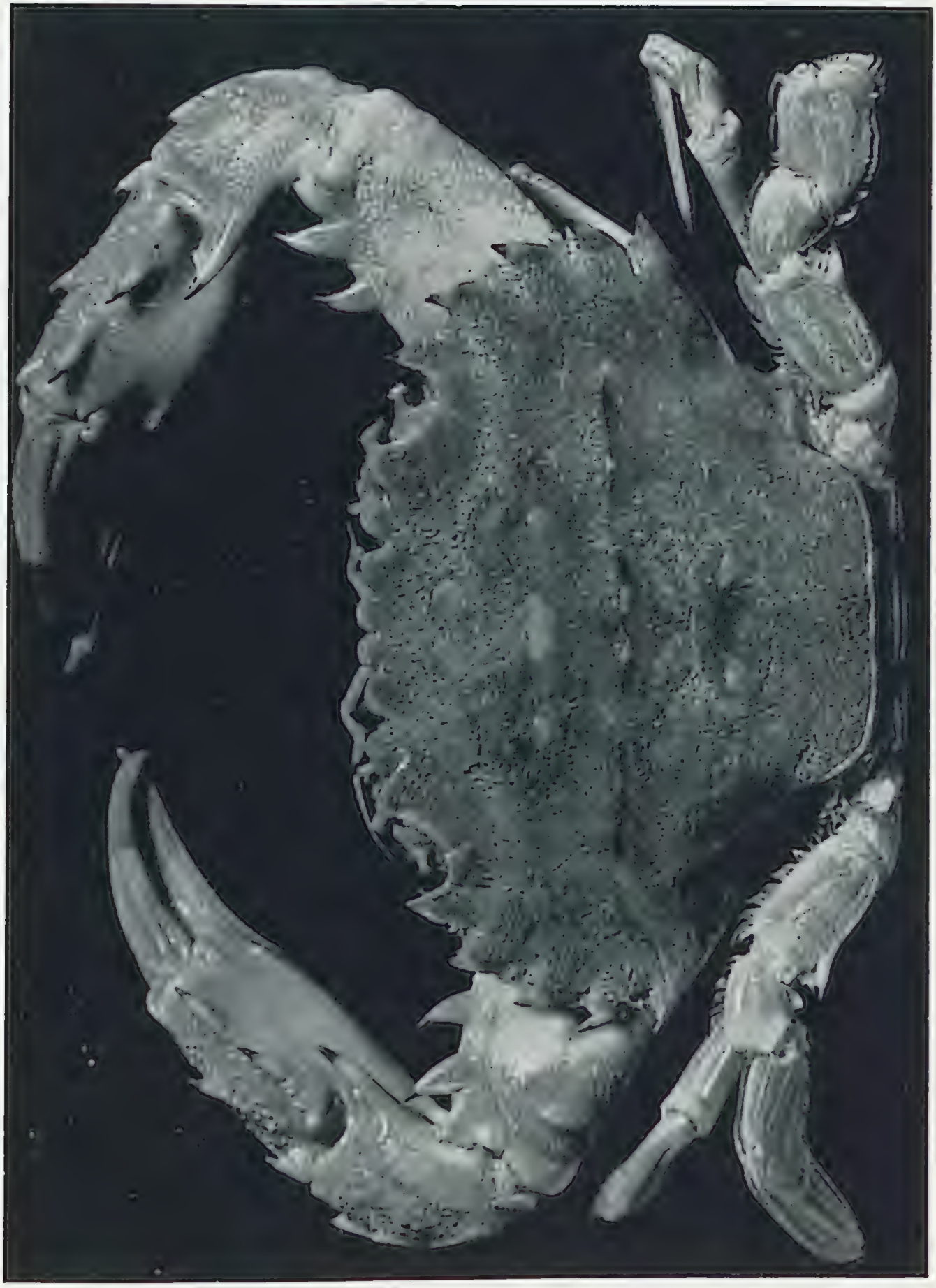

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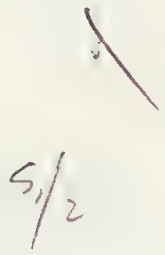
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